SPECIAL COLLECTOR'S EDITION

SCIENTIFIC AMERICAN

AUTUMN 2016

THE STORY OF US

It's stranger than anyone thought

INSIDE

- How Climate Shaped Our Evolution
- What Made Us So Smart
- The Origins of Creativity
- Did We Mate with Neandertals?
- When the Sea Saved Humanity

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5,000-YEAR-OLD rock paintings discovered in northern Somalia.

COVER IMAGE: CRAIG CUTLER; THIS PAGE: MOHAMED ABDIWAHAB *Getty Images*

INTRODUCTION

Humanity's Journey

IN 2013 THE WORLD FOLLOWED, VIA TWEETS, BLOGS AND VIDEOS, AS SCIENTISTS NEGOTIATED the underground system of caves known as Rising Star just outside Johannesburg, South Africa. Ultimately the researchers, working under the direction of paleoanthropologist Lee Berger of the University of the Witwatersrand, would bring up more than 1,500 bones and bone fragments belonging to an archaic human species. The team has concluded that the fossils represent a previously unknown relative of ours, now named *Homo naledi* (*page 12*).

The Rising Star find is only one in a rash of recent discoveries that has extended—and revised—the complex story of human evolution. New fossils are adding branches to our family tree; climate data are revealing the conditions under which the predecessors of our own species evolved their hallmark traits (*page 22*); cognitive studies are homing in on what distinguishes us from our great ape cousins (*page 60*); and DNA analyses are illuminating the extent to which human species interbred (*page 44*)—and how we ourselves continue to evolve.

Arguably, no chapter of the human odyssey has been so dramatically rewritten as the one detailing the ascent of *Homo sapiens.* Far from being an evolutionary slam dunk destined for world domination from the outset, *H. sapiens* no sooner debuted than it nearly went extinct as a result of climate change (*page 36*). Neither is the cognitive divide between *H. sapiens* and archaic species nearly so pronounced as some scholars had envisioned. Discoveries of sophisticated tools and symbolic items reveal that Neandertals were far more technologically advanced and cultured than previously supposed (*page 66*).

In this special edition of *Scientific American,* we explore the evolution of those characteristics that make us human—from our upright stance to our peerless ability to collaborate. Our tale has three chapters. The first examines our tangled family tree and the factors that favored the survival of our branch to the exclusion of others. The second takes stock of how humans differ from other primates—from hairless skin (*page 52*) to unmatched creativity (*page 86*) to widespread monogamy (*page 74*)—and considers how these features may have set us up to thrive. The third ponders the future of human evolution in a world brimming with technological fixes for everything from loneliness (*page 96*) to disease (*page 100*).

We hope you enjoy this story, seven million years in the making. It is not the final word, of course. Just as human evolution seems to be accelerating, so, too, is the pace of paleoanthropological discovery. But we wouldn't have it any other way.

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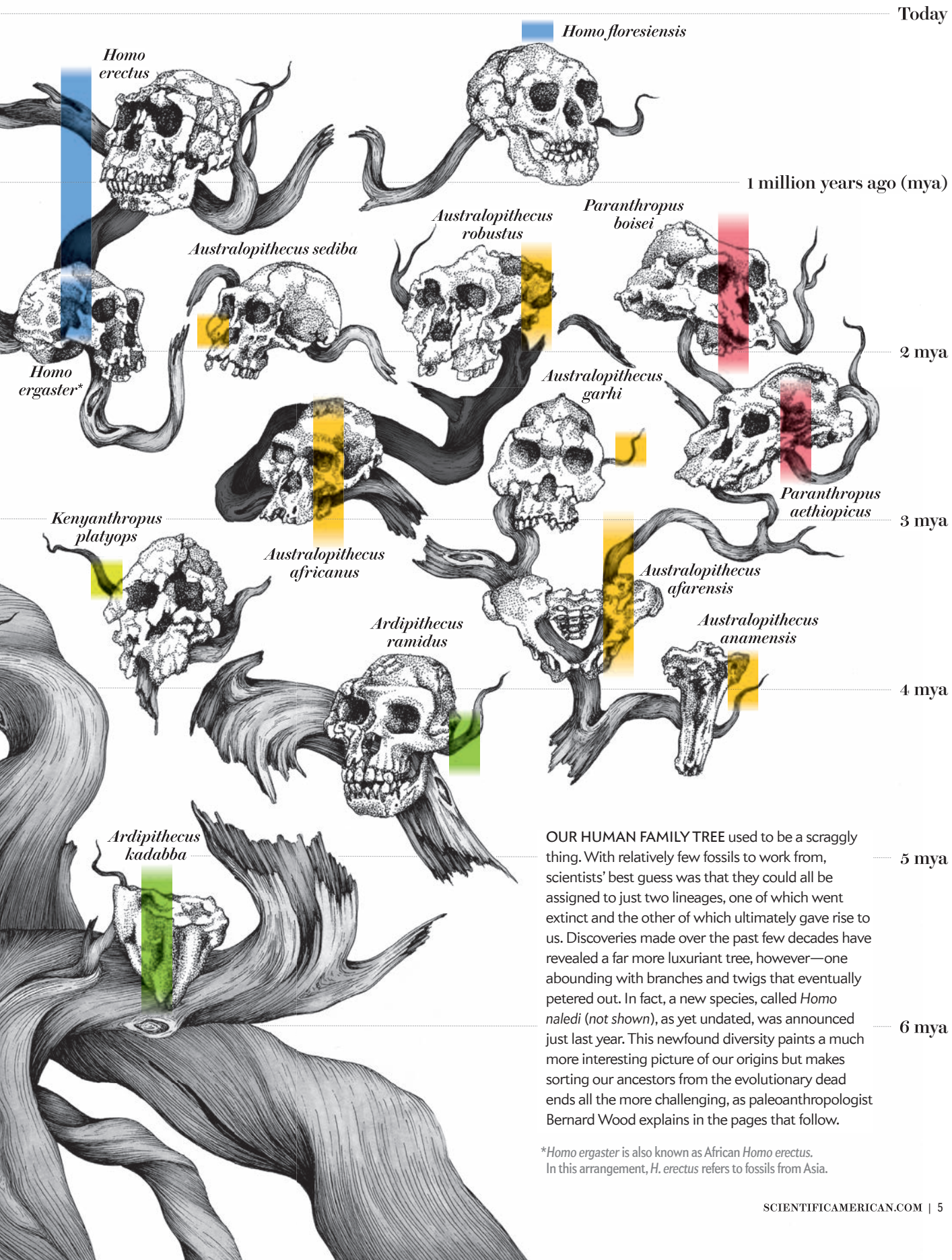
Where We Came From

Illustration by Katy Wiedemann



OUR HUMAN FAMILY TREE used to be a scraggly thing. With relatively few fossils to work from, scientists' best guess was that they could all be assigned to just two lineages, one of which went extinct and the other of which ultimately gave rise to us. Discoveries made over the past few decades have revealed a far more luxuriant tree, however—one abounding with branches and twigs that eventually petered out. In fact, a new species, called *Homo naledi* (*not shown*), as yet undated, was announced just last year. This newfound diversity paints a much more interesting picture of our origins but makes sorting our ancestors from the evolutionary dead ends all the more challenging, as paleoanthropologist Bernard Wood explains in the pages that follow.

**Homo ergaster* is also known as African *Homo erectus*. In this arrangement, *H. erectus* refers to fossils from Asia.*

SOURCE: BERNARD WOOD; FOSSILS NOT DRAWN TO SCALE

Welcome to the Family

The latest molecular analyses and fossil finds suggest that the story of human evolution is far more complex—and more interesting—than anyone imagined

By Bernard Wood

"SO WHAT DO YOU THINK?" SAID LEE BERGER. HE HAD JUST OPENED THE LIDS of two big wood boxes, each containing the carefully laid out fossilized bones of a humanlike skeleton from Malapa, South Africa. These two individuals, who had drawn their last breath two million years ago, had created quite a stir. Most fossils are "isolated" finds—a jawbone here, a foot bone there. Scientists then have to figure out whether the pieces belong to the same individual. Think of walking down the highway and finding parts of cars—a broken fender here, part of a transmission there. Do they belong to the same model, or even make, of car? Or might they not have come from a car at all but from a pickup?

Illustration by Christian Northeast

In contrast, the skeletons from Malapa, though not complete, are intact enough to reduce the possibility of random commingling. Like "Lucy" (unearthed in Ethiopia in 1974) and the "Turkana Boy" (found in Kenya in 1984), they have so much more to say than individual fossils. But they had made the headlines not because they are complete and so well preserved but because Berger, a paleoanthropologist at the University of the Witwatersrand, Johannesburg, had suggested that the individuals were part of a population that was directly ancestral to our own genus, *Homo*.

We all have ancestors. I still have an aged living parent. I had the good fortune to have known all four of my grandparents, and I can even dimly remember three of my great-grandparents. But I also have close relatives who are not ancestors. Not many—my father and I were both only children—but I did have a couple of uncles and aunts. They are an essential part of the family tree of their descendants, but in terms of my family tree they are the equivalent of "optional extras" on an automobile. So Berger wanted me to stop admiring the details of the teeth and jaws and tell him if I thought the Malapa skeletons were the evolutionary equivalent of my parents and grandparents or of my uncles and aunts. In other words, did they belong to a population that was a direct ancestor or just a close relative of modern humans?

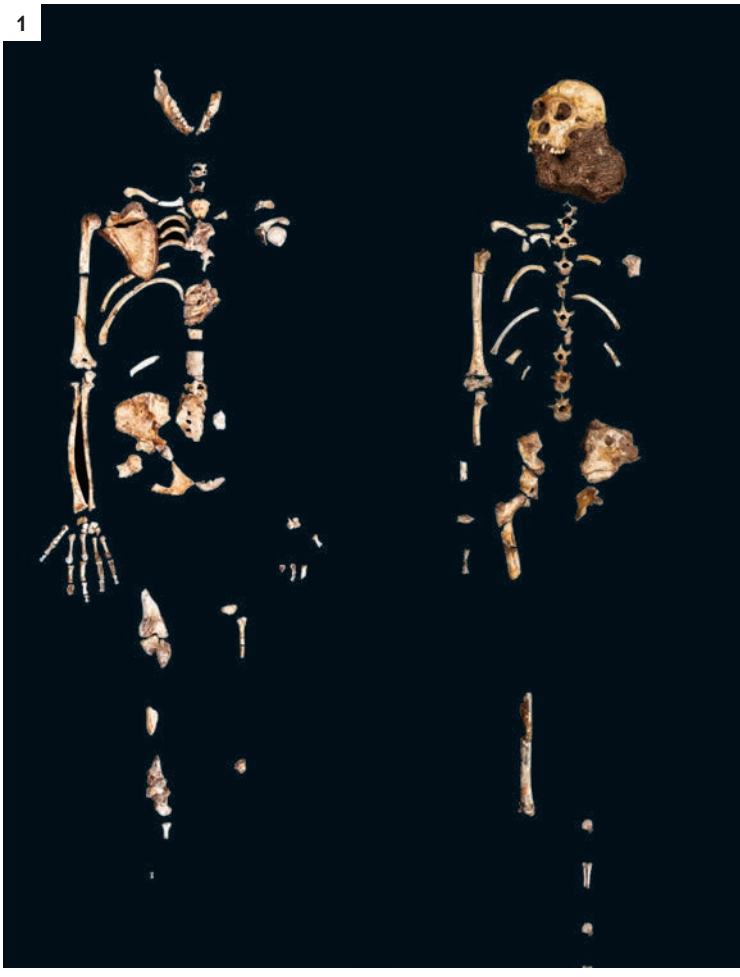
When I first started studying human fossils in East Africa nearly 50 years ago, the conventional wisdom was that almost all of our extinct close relatives were direct ancestors, and as you went further and further back into the past each was less humanlike and more apelike. But we now know from genetic studies and from fossil evidence of the Neandertals and the so-called Hobbit of Flores, Indonesia (*Homo floresiensis*), that our direct ancestors shared the planet over the past few hundred thousand years with several of our close relatives. Furthermore, other fossil discoveries make it clear that much earlier in our prehistory (four million to one million years ago) there were also periods when our ancestors and several close relatives walked the earth at the same time. The presence of multiple evolutionary branches at any one time makes it much more difficult to identify direct ancestors of modern humans than paleontologists anticipated even 20 years ago. Yet the challenge also means that the story of human evolution is far more intricate and fascinating than most of us realized.

A SINGLE BRANCH—OR SEVERAL?

AT THE TIME I entered the field in 1968, Charles Darwin's conception of the Tree of Life held firm sway. In the 1800s Darwin had argued that the living world is linked in the same way that the branches of a tree are connected. In Darwin's Tree of Life, all the species alive today sit on the outer surface of the tree, and all the species that are no longer living are located closer to the trunk. Just as each individual modern human must have ancestors, so does each species alive today. In theory, then, the only branches, or lineages, that *must* be in the Tree of Life are the ones that lead from a living species down into the depths of the tree, and the only extinct species that *have* to be within the Tree of Life are the ones situated on those connecting branches; any others represent evolutionary dead ends.

In the case of modern humans and the living apes, this rule means the only branches and species that need to be in our particular part of the tree are the ones that link us to the common ancestor we share with chimpanzees and bonobos—a creature now thought on the basis of molecular evidence to have lived between about eight million and five million years ago.

In the 1960s the outermost branch of the Tree of Life leading to modern humans looked pretty straightforward. At its base was *Australopithecus,* the ape-man that paleoanthropologists had been recovering in southern Africa since the mid-1920s.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IN BRIEF

Tracing the evolutionary ancestors of *Homo sapiens* was once thought to be a relatively straightforward matter: *Australopithecus* begat *Homo erectus,* which begat Neandertals, which begat us.

Over the past 40 years fossil finds from East Africa, among other discoveries, have completely shattered that hypothesis.

The latest evidence shows that several different hominin species shared the planet at different times. Figuring out how they are all related—and which ones led directly to us—will keep paleontologists busy for decades to come.

TREASURE TROVE: Two nearly complete fossilized skeletons (*1*) of early hominins from two million years ago were recovered from Malapa Cave in South Africa. Researchers are excavating the site (*2*).

BRENT STIRTON *Getty Images Reportage (1 and 2)*

Australopithecus, the thinking went, was replaced by the taller, larger-brained *Homo erectus* from Asia, which spread to Europe and evolved into the Neandertals, which in turn evolved into *Homo sapiens* (aka modern humans). All these were interpreted as direct ancestors of modern humans—the equivalent of my parents, grandparents and great-grandparents. Only one type of hominin (modern humans and any extinct relatives that are more closely related to humans than to chimpanzees or bonobos), called the robust australopiths because of their large jaws and chewing teeth, were surmised to be on a short twig of the human branch and thus the equivalent of my uncle and aunt.

This thinking changed when Louis and Mary Leakey's discoveries of hominins at Olduvai Gorge in Tanzania shifted the focus of research on early hominins that lived more than one million years ago from southern Africa to East Africa. The focus changed not only because the trickle of fossil discoveries in East Africa in the early 1960s turned into a torrent but also because the context of the fossil evidence in East Africa—particularly with respect to its dating—was very different from that in southern Africa.

In the south, the hominin fossils were—and still are—mostly found in caves that form in rocks made of dolomite (a magnesium-rich carbonate). Although researchers occasionally find a well-preserved skeleton of an individual (such as those from Malapa), most of the early hominin fossils found in these caves were leftovers from the meals of leopards and other predators. These unconsumed bones and teeth were washed into the cave along with soil from the surface. Once inside the cave, the soil and bones formed what are called talus cones. These are untidy versions of the neat cones of sand in the bottom of an old-fashioned egg timer, and the layers, or strata, in the cave do not always follow the general rule that the older layers are at the bottom and the youngest at the top. As if this was not frustrating enough, researchers were until recently at a loss to know how to date the sediments in the caves, and in the early 1960s all investigators could do was fit the hominin finds in a very rough-and-ready time sequence based on the types of fossil animals found in the caves.

In contrast, hominin fossil evidence from East Africa comes from sites close to the Eastern Rift Valley, which slices through this part of Africa from the Red Sea in the north to the shores of Lake Malawi and beyond in the south. Instead of being found in caves, the hominin fossils from East Africa are found in sediments laid down around lakes or along riverbanks. Many of these rock layers preserve the direction of the earth's magnetic

field at the time they were laid down, and because they are open-air sites the strata incorporate ash expelled from the many volcanoes generated in and around the Eastern Rift Valley by the movement of tectonic plates. These features mean that at each site researchers have ways of establishing the age of the strata independent of the fossils they contain. In addition, because the layers of volcanic ash function like a series of date-stamped blankets thrown over the region, they allow researchers to correlate fossils deposited hundreds of miles apart.

Many of the richest East African hominin fossil sites, such as those in the Omo-Turkana Basin and farther north along the Awash River, contain strata that represent millions of years of time. Thus, it is possible to give minimum "start" and "finish" dates for each particular group of fossil hominins. This specificity makes it clear that even within East Africa alone, there were many times in the past one million to four million years when more than one—and in some periods, several—hominin species lived contemporaneously. For example, across a million years (from roughly 2.3 million to 1.4 million years ago), two very different kinds of hominins—*Paranthropus boisei* and *Homo habilis*—lived in the same region of East Africa. They were so different that a prehistoric safari guide would have made the point that their skulls and teeth are almost *never* confused, no matter how fragmentary the fossil evidence. It is also clear that the hominins at the sites in East Africa are different from the ones found in southern Africa—but more on that later.

TURKANA FIND: Fossilized skull of a young *Homo ergaster* male that lived and died in Kenya 1.6 million years ago.

KEN GARRETT *National Geographic Creative*

Finding evidence of *P. boisei* and *H. habilis* in the strata that record thousands of years does not necessarily mean the two hominins had to take turns at the same water hole. But it does mean that one, or perhaps both, of these hominins was not ancestral to modern humans. Although evidence from much later in human evolution is consistent with a small amount of interbreeding between Neandertals and modern humans, in my view the much greater physical differences between *P. boisei* and *H. habilis* indicate that interbreeding was much less likely. And even if it did occur, it did little to blur the substantial differences between these two species. In other words, the image of a single, simple branch no longer seems apt for representing humans a couple of million years ago. Our early ancestry looks more like a bundle of twigs—one might even think it looks like a tangled bush [*see illustration on page 4*].

There is also evidence of multiple lineages in our more recent past. For example, Neandertals have been recognized as a separate species for more than 150 years, and as time goes by researchers discover more and more ways in which they differ from modern humans. We also know that a third hominin, namely *H. erectus,* probably survived much later than was originally thought and that *H. floresiensis,* although it may have been confined to the island of Flores, is almost certainly a fourth hominin that lived on the planet within the past 100,000 years. Evidence of a distinctive fifth hominin, the Denisovans, has come from ancient DNA extracted from a 40,000-year-old finger bone. And evidence has emerged for at least one more "ghost lineage" in the DNA of living modern humans from 100,000 years ago. Further, a huge trove of still undated fossils from a species called *H. naledi* was also discovered by Berger in 2013. Thus, our recent evolutionary history is much "bushier" than people thought even a dozen years ago.

Perhaps the discovery of bushiness in our evolution should not have been surprising. Contemporary existence of multiple related species seems to have been the rule in the past for many groups of mammals, so why should hominins have been any different? Still, critics of the bushy family tree have charged that paleoanthropologists have been overzealous in identifying new species from their finds—presumably out of a desire for fame and further research funding.

My prejudice, on the other hand, is that we are most likely dealing with a real phenomenon. First, there are sound, logical reasons to suspect that the fossil record always underestimates the number of species. Second, we know from living animals that many uncontested species are difficult to distinguish using the bones and teeth—the so-called hard tissues, which is all that survives into the fossil record. Furthermore, most of the mammal species that were living between three million and one million years ago have no direct living descendants. Therefore, the existence of several contemporary early hominins with no direct living descendants is not "odd" after all.

If it is true that hominins had rich diversity in their past, it behooves biologists to uncover the evolutionary pressures that triggered it. Climate is one of the obvious candidates; climates, and thus habitats, change over time—they show trends, and they oscillate within those trends. By and large over the period we are considering, there is a trend toward cooler and drier conditions, but within that trend the climate oscillates at predictable intervals, so at times it will be hotter and wetter, and at other times it will be cooler and drier. The type of posture, diet and locomotion that worked at one time may not have been successful at another. Another pressure favoring hominin diversity may have been competition among hominins; if two hominins shared a habitat, even in a very general sense, they would have tended to force each other into different survival strategies. This phenomenon, called character displacement, may explain how *H. habilis* and *P. boisei* came to have such different teeth and jaws—with one group favoring tough, fibrous foods such as grasses and the other leaning toward a diet that included softer, but harder to find, fruits plus the occasional meal of meat or bone marrow. Moreover, as hominins evolved different cultures, their different worldviews and practices could have militated against species interbreeding and eventually merging.

In addition to anatomical differences, researchers can now analyze fossils on a molecular level. Yet when it comes to early hominins—for whom we do not yet have genetic evidence—distinguishing the equivalent of my parents, grandparents and great-grandparents from the equivalent of my uncles and aunts remains challenging. Just because two fossils have similarly shaped jaws or teeth does not mean they share a recent evolutionary history. These overlaps can occur because similar ecological challenges prompt similar morphological solutions. By way of illustration, consider an ax design that works as well to cut down gum trees in Australia as it does to fell spruce in northern Europe; Australians and Europeans could well have hit on the same design without one group having introduced it to the other. We also know that morphology is not infinitely evolvable—for any type of animal or plant, there are a finite number of anatomical or physiological solutions to the same ecological challenge. Thus, the discovery of a shared feature in fossils from two species does not necessarily mean that they are direct taxonomic buddies; they could merely be close relatives that have converged on the same physical solution to a similar ecological challenge.

So what does the future hold for identifying our direct ancestors? I am willing to go a step further than supporting the view that many hominin species roamed the planet simultaneously. I predict that the increased hominin diversity that has been discovered and dated to the past four million years will be shown to extend back even further. I think this in part because researchers have not been looking as long or as hard for hominins that lived in even earlier times. Consequently, they have explored fewer sites from before four million years than after. Admittedly, the work is hard. Hominins are among the scarcest mammals in the fossil record. You have to sort through a lot of pig and antelope fossils before you can expect to find the occasional hominin. But if we make a concerted effort to find them, they will surely turn up.

GENETIC AND FOSSIL EVIDENCE SHOWS CLOSELY RELATED HOMININ SPECIES SHARED THE PLANET MANY TIMES IN THE PAST FEW MILLION YEARS, MAKING IT MORE DIFFICULT TO IDENTIFY DIRECT ANCESTORS OF MODERN HUMANS THAN SCIENTISTS ANTICIPATED EVEN 20 YEARS AGO.

Another reason to predict that more early hominin species remain to be discovered: the fossil records of the more common mammals have nearly as many lineages before three million years as they do after that time. Why would we would not expect hominins to show the same pattern? Finally, existing early hominin sites cover no more than 3 percent of the landmass of Africa, probably less. It is unlikely that such a small geographical sample has managed to capture evidence of all the early hominin species that ever lived on that continent.

And yet each new discovery from before four million years most likely will bring even less certainty. The closer you get to the split between the human and the chimpanzee-plus-bonobo lineages, the more difficult it will be to tell a direct human ancestor from a close relative. It will also be harder to be sure that any new species is a hominin rather than an ancestor of chimpanzees and bonobos or even a species belonging to a lineage that has no living representative. If paleoanthropology is challenging and difficult now—and I remain to be convinced that the Malapa skeletons, representing a new species that Berger later named *Australopithecus sediba,* were direct human ancestors—it is only going to get more so in the future. But it is these challenges that make the field so fascinating. SA

Bernard Wood is a medically trained paleoanthropologist at George Washington University. His interest in human evolution research began in 1968, when as a medical student, he joined Richard Leakey's expedition to northern Kenya.

MORE TO EXPLORE

Fossils Raise Questions about Human Ancestry. Ewen Callaway in *Nature*. Published online September 8, 2011.

Human Evolution: Fifty Years after *Homo habilis*. Bernard Wood in *Nature,* Vol. 508, pages 31–33; April 3, 2014.

What Does It Mean to Be Human? Smithsonian Institution's Human Origins Initiative: http://humanorigins.si.edu

scientificamerican.com/magazine/sa

NEW HUMAN SPECIES: *Homo naledi* raises questions about the origin and evolution of our genus. In this replica of the composite skull, white areas indicate missing bone.

Mystery Human

An astonishing trove of fossils has scientists, and the media, in a tizzy over our origins

By Kate Wong

THE STORY OF US

IN BRIEF

In 2013 cavers discovered a cache of enigmatic fossils deep inside an underground cave system known as Rising Star near Johannesburg, South Africa.

Over the course of two expeditions scientists recovered more than 1,550 specimens belonging to at least 15 individuals from the site.

In September 2015 researchers unveiled the discovery to great fanfare, announcing that the bones represent a new species, *Homo naledi*, that calls into question long-standing ideas about the rise of *Homo*.

Critics have raised concerns about the recovery and analysis of the fossils.

IN THE BRAND-NEW FOSSIL VAULT AT THE UNIVERSITY OF THE WITWATERSRAND, JOHANNESBURG, in South Africa, shelf space is already running out. The glass-doored cabinets lining the room brim with bones of early human relatives found over the past 92 years in the many caves of the famed Cradle of Humankind region, just 40 kilometers northwest of here. The country's store of extinct humans has long ranked among the most extensive collections in the world. But recently its holdings doubled with the discovery of hundreds of specimens in a cave system known as Rising Star. According to paleoanthropologist Lee Berger and his colleagues, who unearthed and analyzed the remains, they represent a new species of human—*Homo naledi,* for "star" in the local Sotho language—that could overturn some deeply entrenched ideas about the origin and evolution of our genus, *Homo*.

Berger is camera-ready in a brown leather blazer and set to give his spiel to the dozen or so journalists, including me, gathered around him in the vault in late 2015. He directs the visitors' attention to the six black carrying cases—originally made to hold assault rifles—arrayed on tables around the room. Each contains a dizzying assortment of fossils nestled in its foam-lined interior. In the cabinets along the back wall, more *H. naledi* bones fill dozens of clear plastic containers labeled "cranial fragments," "pelvis," "radius." Berger reaches into case number two, which holds the crown jewels of the Rising Star assemblage—the group of bones that defines the species—and lifts out an upper jaw and a lower jaw. He carefully holds them one atop the other and displays the matched pair with a practiced flourish so that everyone gets a good look. The crowd murmurs appreciatively, pens scribble, camera shutters click, flashes pop. And he glides on to the next specimen, fielding questions, posing for photographs and encouraging the visitors to snap selfies with the vault's celebrity charges.

Just a few decades ago the sum total of fossils belonging to our extinct human relatives, also called hominins, could fit in a desk drawer. Those destitute days are long gone. Scientists have since amassed more evidence of the evolutionary history of the human family than of many other animal groups, including our closest living relatives, the great apes. As a result, they now know, for example, that humanity's roots reach back at least seven million years and that for much of that time our ancestors shared the planet with other hominins.

Yet they still have much to learn. Some chapters of the human story are completely unknown from the fossil record; others have been drafted on the basis of evidence so scanty that they are little more than speculation. And so even though the fossil record of humans is vastly bigger than it once was, it is still imperfect enough that new discoveries often alter scientists' understanding of the details of humanity's past—sometimes significantly so.

The Rising Star fossils are the latest to rock the paleoanthropology establishment. Berger and his team argue that *H. naledi* could illuminate the long-sought roots of *Homo* and revamp the human family tree. What is more, the researchers suggest, this creature, which had a brain the size of an orange, engaged in ritual behavior previously attributed exclusively to much brainier hominins—a finding that could upend the prevailing wisdom linking cognitive sophistication to large brain size.

HOLE IN THE GROUND: Fossils of *Homo naledi* were found in a cave in South Africa's Cradle of Humankind.

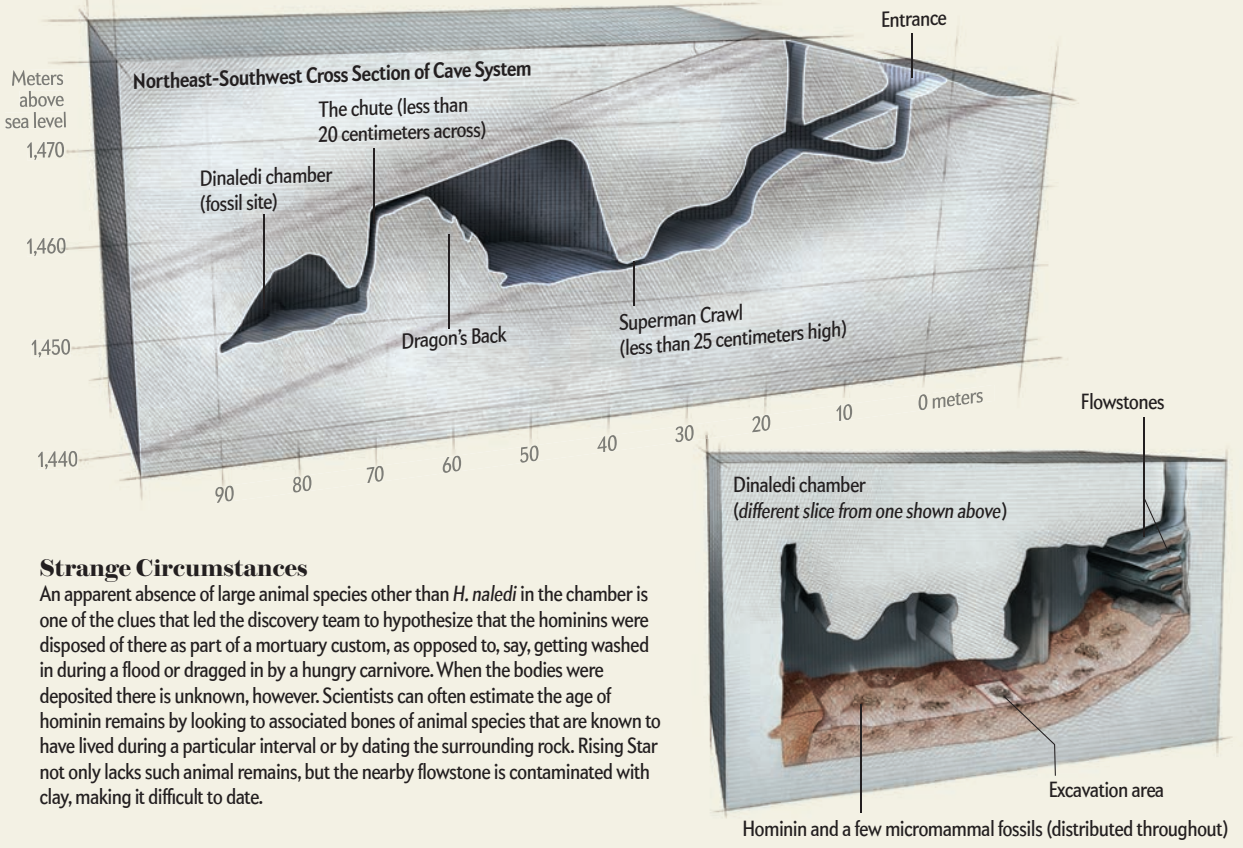
Some critics have dismissed these claims outright. Others have greeted them with uncharacteristic reticence. One major stumbling point for many is that the age of the bones is unknown. They could be more than four million years old or less than 100,000 years old. The lack of a date is not the only concern weighing on outside observers, however. The way the fossils were unearthed, analyzed and revealed to the rest of the world has vexed some of the field's leading scholars, who charge that Berger and his colleagues rushed the job and prioritized publicity over science. In a field known for its fierce rivalries, heated debate over

PAGE 12: COURTESY OF JOHN HAWKS AND UNIVERSITY OF THE WITWATERSRAND, JOHANNESBURG; RECONSTRUCTION BY PETER SCHMID *University of the Witwatersrand;* THIS PAGE: COURTESY OF MARINA ELLIOTT *University of the Witwatersrand*

LOCATION

Chamber of Bones

Cavers discovered the fossils of the new human species *Homo naledi* in an underground cave known as Rising Star, just outside Johannesburg, South Africa (*right*). The bones come from the so-called Dinaledi chamber, which sits 30 meters below the surface. To reach it, excavators had to undertake steep climbs and squeeze through tight passages (*below*). *H. naledi* may have taken similar pains to get there: researchers think it may have been intentionally disposing of its dead in the chamber (*inset*), and although geologists are still working to understand how the cave evolved over time, they have yet to identify other plausible routes into the chamber.



Strange Circumstances

An apparent absence of large animal species other than *H. naledi* in the chamber is one of the clues that led the discovery team to hypothesize that the hominins were disposed of there as part of a mortuary custom, as opposed to, say, getting washed in during a flood or dragged in by a hungry carnivore. When the bodies were deposited there is unknown, however. Scientists can often estimate the age of hominin remains by looking to associated bones of animal species that are known to have lived during a particular interval or by dating the surrounding rock. Rising Star not only lacks such animal remains, but the nearby flowstone is contaminated with clay, making it difficult to date.

SOURCE: "GEOLOGICAL AND TAPHONOMIC CONTEXT FOR THE NEW HOMININ SPECIES *HOMO NALEDI* FROM THE DINALEDI CHAMBER, SOUTH AFRICA," BY PAUL H.G.M. DIRKS ET AL., IN *ELIFE*, ARTICLE NO. 09561; PUBLISHED ONLINE SEPTEMBER 10, 2015

new finds is the norm. But there is more on the line in the row over the Rising Star remains than a few egos. How scientists respond to this discovery in the longer term could set a new course in the quest for human origins, changing not only the questions they ask but the ways in which they attempt to answer them.

INTO THE DEEP

IN A WAY, it was a set of grainy photographs shown to Berger on October 1, 2013, that sparked this spectacle. Berger had hired geologist Pedro Boshoff to search the Cradle for new hominin sites. Over the years miners and fossil hunters had combed the region many times over. But Berger had good reason to think there was more to find. Five years earlier his then nine-year-old son had stumbled across bones of a previously unknown member of the human family, *Australopithecus sediba,* right in the middle of the Cradle.

Now Boshoff and local cavers Rick Hunter and Steven Tucker had found what appeared to be human bones littering the floor of an extremely difficult-to-reach chamber 30 meters down in the Rising Star cave system, just a few kilometers from the spot where Berger and his son had found *A. sediba*. The explorers had not collected any of the material, but they had taken pictures. As soon as Berger saw them, he knew the bones were important. They had features that clearly differed from those of anatomically modern humans—*Homo sapiens*. And there were lots of them, enough to represent a skeleton.

Berger immediately began making plans to recover the remains. There was a problem, though. He was not going to be able to collect them himself. The route from the cave entrance to the chamber that held the bones contained passages far too narrow to accommodate Berger's broad frame or that of most of his scientist colleagues for that matter. Widening these passages would disrupt the integrity of the cave and possibly damage the bones—a nonstarter, as far as he was concerned. So he put out a call on

Illustration by José Miguel Mayo

1

2

Facebook for skinny scientists who had experience caving and excavating old remains and who could come to Johannesburg on short notice to mount an expedition in exchange for little more than a plane ticket and the promise of adventure.

Five weeks after Boshoff showed him the tantalizing photographs, Berger had selected his team of excavators—all women, coincidentally—to carry out the difficult, dangerous work of recovering the bones from the chamber, as well as a crew to support the team's efforts; he developed a protocol for collecting the material and documenting exactly where in the chamber each piece of bone came from; and he established a group of senior scientists to oversee the excavation via closed-circuit television and to identify, log and store the specimens as they came out. He also had a plan for how to publicize the endeavor—a full-bore media blitz, carried out in partnership with *National Geographic* and *NOVA,* that would include live tweets and daily blogs, radio interviews and video clips posted from the field, as well as a TV documentary that would air at a later date, after the remains were eventually published. On November 10, cameras rolling, the excavators crawled, climbed and wriggled their way into the pitch-dark chamber and began the recovery effort.

Marina Elliott was the first scientist to enter the chamber. "I didn't know what to expect, but I was excited," she recalls when I accompany her to the Rising Star site. It is high noon on a bright, hot austral summer's day, and outside the cave the wind carries the sound of cars whizzing past on the nearby freeway. But inside the cave it is dim and cool and hushed—the stillness of age. A shaft of light from a natural opening in the ground above bathes the craggy interior, giving it the air of a place of worship.

The serenity of this part of the cave belies the danger farther in, however. Elliott shines her flashlight down one of the corridors, illuminating a perforated curtain of limestone. Behind that wall lies the first of the squeeze points on the route into the fossil chamber, she explains—the Superman Crawl, a tunnel that the women had to negotiate belly to ground and one arm outstretched. The journey did not get easier from there. A jagged ridge called the Dragon's Back loomed ahead, followed by a 12-meter-long, vertical chute less than 20 centimeters (eight inches) across that opened into the chamber of bones.

But their efforts were richly rewarded. There were bones everywhere—much more than the single skeleton Berger had expected to salvage. Over the next 21 days Elliott and her colleagues hauled out 1,200 specimens. A second, shorter expedition in March 2014 yielded several hundred more. In total, the team recovered more than 1,550 bones and bone fragments of at least 15 individuals—including infants, tweens, young adults and old-timers—from an area the size of a card table. All told it is one of the largest single assemblages of hominin fossils ever found. And the team only scratched the surface. More bones, possibly thousands more, remain in the chamber.

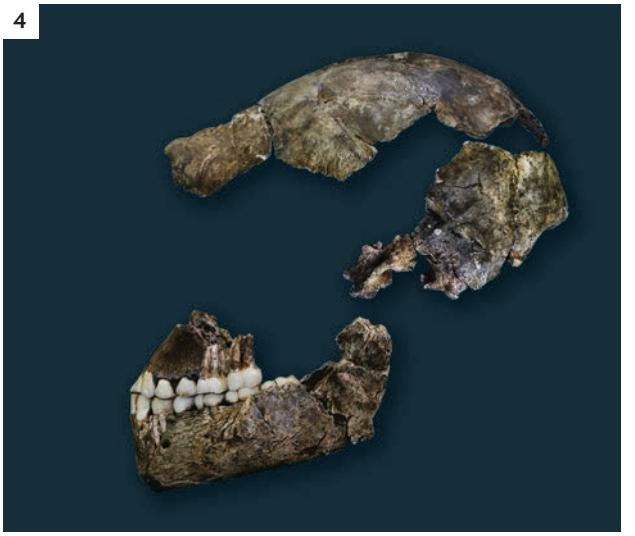
A STAR IS BORN

WITH SAFE AFTER SAFE stuffed with hominin fossils, Berger and his colleagues now faced the daunting prospect of assessing them. Even before the researchers began their formal assessment, while the bones were still coming out of the ground, the find had an air of mystery about it. For one thing, the bones appeared to have a weird combination of primitive and modern traits. For another, no animal remains apart from those of a few small birds and rodents had turned up in the chamber along with the hominin bones. Larger animals such as monkeys, antelopes and hyenas almost always accompany hominin fossils, particularly those found in underground caves. The absence of such species at Rising Star demanded explanation.

Berger recruited an army of 35 early-career researchers to help describe the fossils over the course of a monthlong workshop in Johannesburg in May 2014. For most of these people—many still working on their Ph.D.s—it was a rare opportunity to work on new fossils, as opposed to studying material that had already been characterized by other, more seasoned scientists. They worked in groups organized by body part: skull, hand, teeth, spine, hip, leg, foot, and so forth. When they pooled their findings, a startling picture emerged of a tall, slender hominin with upper limbs built for climbing and using tools, lower limbs built for upright striding and a teeny brain. It is "a really, really strange creature," Berger says.

On a Friday afternoon in December, senior team member John Hawks of the University of Wisconsin–Madison takes me

COURTESY OF JOHN HAWKS AND UNIVERSITY OF THE WITWATERSRAND



HEAD TO TOE: Vast Rising Star fossil assemblage includes rare foot bones (*1*) and multiple leg bones (*2*). Though fragmentary, the fossils are beautifully preserved and can in some instances be attributed to the same individual, as is the case for the lower jaw (*3*) and skull fragments (*4*).

back to the vault to point out some of the salient aspects of the Rising Star remains. The rest of his colleagues are still outside enjoying beer and barbecue at the department holiday party, but Hawks is in his element here among the bones. He bustles around the room, setting the fossil cases out on the tables and selecting replicas of other hominin specimens from the vault's vast collection for comparison.

The skull exhibits a mishmash of traits associated with various hominin species. It would have held a brain measuring just 450 to 550 cubic centimeters—as small as that of primitive *Australopithecus afarensis,* best known from the 3.2-million-year-old Lucy skeleton, found in 1974 in Ethiopia. Yet the shape of the skull evokes the more humanlike *Homo erectus.* The teeth resemble those of *Homo habilis,* one of the most primitive members of our genus, in the way they increase in size from the front of the tooth row to the back. But overall the teeth are small, and the molars have simple crowns with fewer, lower cusps—traits associated with later *Homo.*

The bones below the head echo the mix-and-match theme. The upper limb pairs a shoulder and fingers adapted to climbing with a wrist and palm built for manipulating stone tools—an activity that was not thought to become important to hominins until after they had abandoned life in the trees and evolved large, inventive brains. And the lower limb marries a Lucy-like hip joint to a foot that is virtually indistinguishable from our own. Researchers have been operating under the assumption that the signature features of *Homo*—such as a toolmaking hand, big brain and small teeth—evolved in concert. "*Sediba* and *naledi* show that things we thought we evolved together did not," Hawks asserts. (Like *H. naledi*, *A. sediba* displays a startling mix of traits.)

This unprecedented combination of primitive and modern features is not the only distinctive thing about *H. naledi*. The fossils also have traits never before seen in a member of the human family. Hawks plucks one of the finger bones out of its foam cutout. It is the first metacarpal, the bone in the palm that sits below the thumb, and when he displays it next to the same bone from *H. sapiens,* the difference is stark. The shaft of its first metacarpal is smooth, thick and broad for its entire length. *H. naledi*'s, in contrast, is narrow at the base and broad at the top, with a sharp crest running along its shaft and thin wings of bone on the sides. The femur bears unique traits, too, as do other elements.

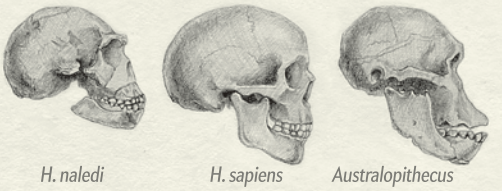
To Berger and his colleagues, the novel combination of australopithecine and *Homo* characteristics, along with the presence of unique traits, easily justified assigning the Rising Star fossils to a new hominin species. Although the researchers have yet to establish the age of the fossils, in one of two papers announcing the find, published in September 2015 in the online open-access journal eLife, they proposed that, given its primitive features compared with early *Homo* species such as *H. habilis* and *H. erectus, H. naledi* might be older than two million years and stem from the base of the genus *Homo.* If so, the discovery would be a major coup: the origin of *Homo* is arguably the biggest unsolved mystery in all of human evolution because fossils transitional between the australopithecines, with their many apelike traits, and later *Homo,* with its modern body plan, are exceedingly rare and mostly scraps. Scientists have been eager to elucidate which hominin species founded the *Homo* branch of the hominin family tree and how the traits in the modern human body plan evolved with new discoveries.

Berger's team did not stop at saying the find could bear on the origin of *Homo,* however. It argued that the unexpected mix of traits evident in *H. naledi* implies that isolated fragments cannot be used to understand the evolutionary relationships of fossil humans, because the part cannot predict the whole—fighting words to those researchers who have interpreted isolated bones as the earliest evidence of the *Homo* lineage.

Perhaps even more provocative than the team's ideas about what *H. naledi* means for understanding hominin relationships is how it interpreted *H. naledi*'s behavior. In their attempts to figure out how the hominins ended up in the chamber, the researchers considered a number of mechanisms known to account for hominin accumulations at other sites, including the possibility that their bones had washed into the cave system

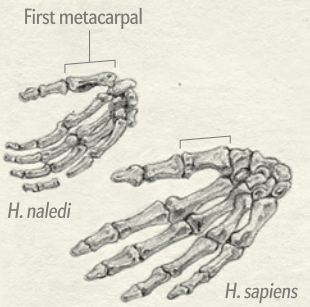
A Novel Mix

The excavations at Rising Star have yielded more than 1,550 fossil specimens of *Homo naledi* belonging to at least 15 individuals ranging from infants to oldsters. Nearly every bone in the body is represented in the collection, many of them more than once. From these remains scientists have reconstructed a creature with a startling combination of traits associated with the primitive australopithecines and traits seen in various species in our genus, *Homo*, as well as some traits not known from any other hominin species. Examples of these features are highlighted in the diagram below.



Skull of *H. naledi* housed a brain as small as 450 cubic centimeters—a size that is typical for australopithecines but significantly smaller than the brains of *H. sapiens* and most other members of *Homo*.

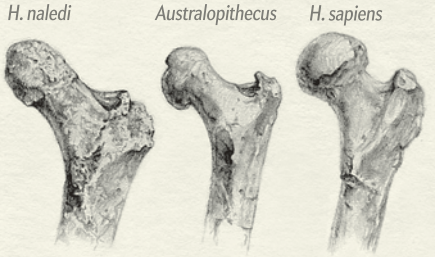
Teeth are primitive in the way they increase in size from front to back. Overall they are small, and the molars have comparatively simple cusps—both traits of later *Homo* species.



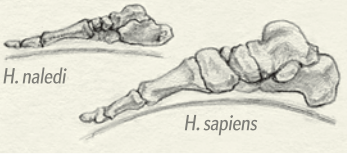
Hand has strongly curved fingers, suggesting that *H. naledi* climbed in trees. Yet the wrist and palm look modern and appear to be adapted to manipulating tools. For its part *H. naledi*'s first metacarpal, the bone in the palm below the lowermost thumb bone, looks neither *Homo*-like nor *Australopithecus*-like and is utterly unique.

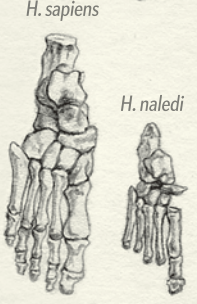
Shoulder socket faces up like an ape's or australopithecine's rather than out to the side like ours does. This upward orientation is an adaptation to climbing trees.

Femur has a small head and long neck compared with the large head and small neck seen in the *Homo sapiens* femur. These features suggest that *H. naledi*'s hip worked like an australopithecine's.



Foot is remarkably like our own, apart from the slightly curved toes and somewhat lower arch, and thus well adapted to upright striding. But the combination of this modern foot and the primitive hip means *H. naledi* would have walked differently from us.





A New Twig in Our Tree

The discovery team argues that *H. naledi*'s particular mix of characteristics suggests that the species originated close to the origin of *Homo*—a coveted spot in the family tree. But *H. naledi* preserves parts of the anatomy that are not known for other early *Homo* species, complicating efforts to understand how these extinct hominins are related to one another—and to us.

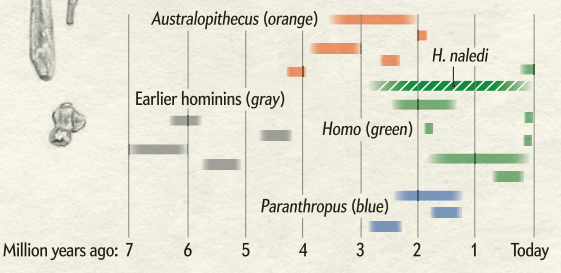


Illustration by Portia Sloan Rollings, Graphic by Jen Christiansen

during a flood or that large carnivores had dragged them there to eat. Yet the available evidence did not match any of those explanations. Floodwaters, for instance, would have surely carried the remains of other animals into the chamber, too. And carnivores would have left behind telltale tooth marks on the bones. All things considered, the team concluded, the likeliest explanation was that *H. naledi* had intentionally deposited the bodies in the chamber.

The hominins would have had to go to considerable lengths to do so. Although the team geologists do not yet know exactly how the Rising Star cave system formed and changed over time, they have found only one entrance to the bone chamber—the one the excavators squeezed through to recover the fossils. If that was indeed the only entrance, then whoever disposed of the dead would have had to, at minimum, scale the 20-meter spine of the Dragon's Back to reach the opening of the chute that opens into the chamber. From there they could have either crawled down the chute with the bodies or just dumped them in and let them slide into the chamber below. And if the route into the chamber was always pitch-dark, as the team thinks it was, then the hominins may have required an artificial light source to find their way in. The suggestion was that tiny-brained *H. naledi* not only had a mortuary ritual but mastery of fire.

Ensconced in a leather club chair in the sitting area of his office, coffee mug in hand, Berger launches into a discussion of what the Rising Star find means for human evolution. It's 7:30 in the morning, but the blinds are drawn, and the lights are low. Between the animal hide rugs decorating the floor and the jazz warbling from a vintage-style turntable, the room feels more like a gentleman's hunting lodge than a work space. "There is no age at which [the find] is not disruptive," he exults. If it is old, then critical physical and behavioral traits may have emerged at the root of our genus or earlier, rather than in later *Homo*. Really old *H. naledi* could even oust the australopithecines from the line leading to us, according to Berger. If, on the other hand, the fossils are young, researchers are going to have to reconsider which species left behind the cultural remains at key archaeological sites across Africa.

It may be *H. naledi* originated millions of years ago and managed to persist across the ages unchanged, like a coelacanth, overlapping with other *Homo* species, including *H. sapiens,* for a time. Perhaps it invented some of the cultural traditions archaeologists have traditionally assumed originated with our kind, Berger says. Possibly *H. naledi* interbred with our ancestors and contributed DNA to the modern human gene pool, like Neandertals and Denisovans did.

CASTING ASPERSIONS

WHEN THE TEAM announced its discovery in eLife last year, the world went wild for *H. naledi*. Seemingly every media outlet on the planet covered the find. Even the *Onion* joined the bandwagon, running a doctored image of a lachrymal Berger with a story entitled "Tearful Anthropologists Discover Dead Ancestor of Humans 100,000 Years Too Late." Yet underneath that tidal wave of public enthusiasm runs a current of discontent among some of paleoanthropology's elite. No one disputes that the find is important—a cave full of human fossils is extraordinary—but the team's approach to recovering, describing and interpreting the bones has raised eyebrows.

Berger is no stranger to side eye from his academic peers. Telegenic and silver-tongued, he hooked up with *National Geographic* early in his career. The relationship brought research funding, bylines and television appearances. Yet he had found few fossils, and his scientific papers and popular writings met with accusations of sloppy scholarship and grandstanding from some of paleoanthropology's most respected figures, including Tim White of the University of California, Berkeley, and Bernard Wood of George Washington University.

Berger's discovery of *A. sediba* in 2008 raised his scientific profile. Even his harshest critics conceded that the find, which included two largely complete skeletons dated to 1.98 million years ago, was spectacular. But many did not agree with his interpretation of it. Berger had long contended that South Africa was being overlooked in favor of East Africa in the search for *Homo*'s origin. *A. sediba,* with a mosaic of australopithecine and *Homo* traits, seemed to offer a means of potentially rooting *Homo* in South Africa. The problem was that the oldest fossils attributed to *Homo* were East African specimens older than *A. sediba*. Berger argued that fossil fragments like the ones from East Africa that were being held up as the earliest *Homo* could no longer be assigned to one taxon or another because his skeletons, with their surprising combination of traits, showed the whole was not inferable from the part. His peers largely rejected that claim.

With *H. naledi,* Berger doubled down on the public outreach and on those controversial ideas about *Homo*'s origin and fragmentary fossils. It did not take critics long to loose their arrows. White told his university's alumni association magazine, *California,* that the Rising Star fossils looked like primitive *H. erectus,* not a new species. White is best known for his discoveries of hominin fossils in Ethiopia, including those of 2.4-million-year-old *Australopithecus garhi,* which he and Berhane Asfaw of the Rift Valley Research Service and their colleagues said were from the right time and place to be ancestral to *Homo*. He further accused the Rising Star team of damaging fossils during excavation and rushing its findings to publication. Later, in a scathing blog post for the *Guardian,* White warned of the dangers of mixing science and showmanship. "We are witnessing portions of science collapsing into the entertainment industry," he wrote.

White is not the only one with concerns. Carol Ward of the University of Missouri cautions that although the quantity of fossils is stunning, their significance remains unknown. She emphasizes the importance of determining the age of the bones: "When we know how old they are, then we can tell you what they mean for human evolution but not until then."

Ward also has misgivings about the paper describing the fossils, noting that it did not include sufficient data about how they compare with other relevant fossils for outside scientists to be able to evaluate many of the team's claims. Nor did the paper contain a phylogenetic analysis—basically a study in which a computer program compares traits across a group of organisms and thereby reconstructs the members' evolutionary relationships—which could reveal where *H. naledi* fits in the human family tree. "There seems to be a great desire [on the part of the authors] for it to be related to the origins of *Homo,*" she observes, but in the absence of a detailed phylogeny or a date, no one can know if it is.

Many researchers stand by the thinking that, based on present evidence, *Homo* debuted in East Africa. Last year, months before the details of *H. naledi* were released, Brian Villmoare of the University of Nevada, Las Vegas, Kaye Reed of Arizona State Uni-

GETTING A GRIP: Hand of *H. naledi* is the most complete one known for an extinct human species.

COURTESY OF JOHN HAWKS AND UNIVERSITY OF THE WITWATERSRAND

versity and their colleagues announced their discovery of a 2.8-million-year-old piece of lower jaw from the site of Ledi-Geraru in northeastern Ethiopia that they say is the earliest known representative of our genus. The jaw has clear hallmarks of *Homo,* they observe, as well as traits transitional between *Australopithecus* and *Homo*. Without a date, the *H. naledi* fossils cannot unseat the Ledi-Geraru jaw as the oldest evidence of our lineage, in Reed's view, nor does she accept the argument made by Berger, Hawks and their colleagues that isolated fragments of anatomy cannot be reliably assigned to one taxonomic group or another. "I have a good date at 2.8, and there are features of *Homo,*" she maintains.

Paleoanthropologists disagree on which fossils herald the dawn of *Homo* partly because they are divided over what constitutes *Homo*. *H. naledi* "highlights an ongoing debate about how to define *Homo,* both for things we have pieces of and things we have more of," comments Susan Antón of New York University, an expert on early members of our genus. Sorting *Homo* from *Australopithecus* is "a very messy thing for everyone right now, and different people have different philosophies about how to make that distinction." She and her collaborators have been defining it on the basis of traits found in the cranium, jaws and teeth. Others have argued that the distinction between the two has to be based on the bones below the head—the postcrania, as they are termed—because they reflect the major adaptive changes hominins underwent as they transitioned from wooded environments to open ones. But those postcranial bones are largely unknown for early *Homo* species. The Rising Star fossils are "an embarrassment of riches," Antón remarks. But the mosaic of traits gives mixed signals, and Berger's team did not explicitly state how it defines *Homo* and why. "We have a lot more talking to do," she says of the field.

Yet even if the Rising Star remains do constitute a new *Homo* species and even if they turn out to be more than two million years old, those facts alone may not be enough to sway the skeptics toward the notion that *H. naledi* was on or near the line leading to us. George Washington's Wood suspects that the bones represent a relic population that might have evolved its odd traits in relative isolation. "South Africa is a cul-de-sac at the bottom of the African continent," he says. "My guess is gene exchange in this cul-de-sac was probably not as common as it was in East Africa, where you have a lot more potential for homogenization, with genes coming in from southern and central Africa." Wood points to another weird species of *Homo*—the small-brained, small-bodied *Homo floresiensis* that persisted on the island of Flores in Indonesia long after *H. sapiens* originated in Africa—as another example of such a relic population.

The suggestion that small-brained *H. naledi* was ritually disposing of its dead has likewise met with resistance. "It would be quite radical," says archaeologist Alison Brooks of George Washington University. The practice is widely thought to be exclusive to the much larger-brained anatomically modern humans and possibly Neandertals and only became commonplace after 100,000 years ago. "I don't want to rule it out entirely that [the Rising Star researchers] are right," Brooks adds, "but I just think it is so far out there that they really need a higher standard of proof."

In fact, some of the discovery team members themselves struggled with the idea that *H. naledi* was deliberately disposing of its dead in that underground chamber, if only for logistical reasons. "It's hard to get in there with my backpack, never mind dragging a body," Elliott reflects. "But we spent two years trying to find an alternative and couldn't."

The debate over how the bones got into the remote chamber intensified in April, when Aurore Val of the University of the Witwatersrand published a critique of the team's interpretation in the *Journal of Human Evolution*. In it, Val, who is not on Berger's team but was his graduate student, argued that because caves can evolve considerably over time, it is impossible to say what Rising Star was like when the fossils landed in the chamber without knowing the age of the bones—there might have been an easier way in. She further contends that the researchers did not study enough of the fossil remains from the site to exclude the possibility that water or carnivore activity played a role in accumulating the bones there.

EYE ON THE PRIZE

BERGER DISMISSES THE DETRACTORS. Staunchly defending the care with which the team excavated the fossils, he explained in a public post on Facebook that the damage on the bones was already there when Rising Star team members first arrived on the scene. Berger presumes it resulted from unknown amateur cavers who had explored the chamber before them and stepped on the bones. The excavators were able to work quickly, he says, because "we didn't have a lot of problems other teams have." At other sites, fossils are typically encased in rock. Excavation and cleaning of such fossils are typically extremely laborious and time-consuming. But at Rising Star the fossils were simply lying

in damp earth that brushed away easily. And unlike other teams, which are small and conduct their research in distant locales six to eight weeks a year, Berger's is large and based in Johannesburg, so it can work at the site or in the vault any time. If you look at the Rising Star work in terms of person-hours logged in the time between discovery and publication, "it's as much as anyone else has done," he insists.

As for White's suggestion that the fossils belong to primitive *H. erectus,* not a new species, "he disagrees with everything except the ones he basically has named," Berger quips. Assigning the *naledi* remains to *H. erectus* would mean that *erectus* had more variation than is seen in our own species, which is improbable, in his view. More to the point, *H. naledi* has unique traits not seen in any other hominin. "If we're going to be evolutionary biologists, the argument stops there," Berger declares. "Frankly I'm surprised [people] aren't arguing that it's a new genus," rather than merely a new species.

Asked about dating the Rising Star fossils, Berger says the geologists are working on it and will get the timing down eventually. But he maintains that the date will not change their understanding of how *H. naledi* is related to other members of the human family. Although *H. naledi* has some key traits of *Homo,* the overall package is in some ways more primitive than that of *H. habilis* and, for that matter, that of the Ledi-Geraru jaw that currently holds the title of oldest *Homo* fossil. No matter what age the Rising Star fossils turn out to be, they imply that *H. naledi*'s branch of the family tree sprouted before these other branches did. If the fossils are young, then they represent a late population of this species.

Why, then, didn't the team include a phylogeny in the paper announcing the fossils as a new species? To figure out how organisms are related to one another, evolutionary biologists use a method called cladistics that sorts taxa into groups based on novel characteristics they share with their last common ancestor but not earlier ones. The catch is, the method works best when the characteristics are observable in all the organisms in question.

Where fossils are concerned, meeting that requirement is easier said than done because they vary widely in the traits they preserve. In paleoanthropology, researchers have tended to base their cladistic analyses on traits found in skulls and teeth: skulls because they vary widely in form in hominins and thus historically were thought to be particularly useful for defining species and teeth because they are the most common elements in the hominin fossil record. Bones from the rest of the skeleton are not always found in association with skulls or teeth, so it can be difficult to assign them to a species that is defined by cranial or dental remains. Moreover, a skeletal element that is known in one species is often missing in another.

Indeed, some of *H. naledi*'s key elements—including its nearly complete sets of hand and foot bones—are only partly represented in the fossil record of other *Homo* species, such as *H. erectus* and *H. habilis,* if they are even represented at all. Lacking corresponding parts with which to compare them, the researchers could not conduct a cladistic analysis of *H. naledi* that factored in its many postcranial traits of interest. With that course of comparison closed off to them, the researchers ran an analysis based on skull and dental traits. But some of the test results did not make logical sense, suggesting that *H. naledi,* with its many primitive traits, is more closely related to *H. sapiens* than to the much older *H. erectus*. To Berger, that finding underscores that trees based on data from one anatomical region, such as the head or teeth, are unreliable. (In a paper published in the August *Journal of Human Evolution,* Mana Dembo of Simon Fraser University in British Columbia and her colleagues reported that a statistical analysis of the *H. naledi* skull and tooth remains supported the link to *Homo* but suggested a considerably younger age of 912,000 years.)

Berger remains certain that *H. naledi* will shake up scientists' understanding of human evolution one way or another. But he is not asking his peers to take his word for it. In a departure from the usual way of doing things in paleoanthropology, which has a reputation for secrecy where access to fossils is concerned, he instituted an explicit policy for the Rising Star remains that makes them available to any researcher who applies to see them. And on the day they published the eLife papers, the researchers released free three-dimensional scans of critical bones on MorphoSource, a digital repository for anatomical data, allowing visitors to print their own 3-D replicas of the specimens. The data resolution is not yet high enough for the purposes of carrying out original research, but "it's good enough to check what we're saying," Berger says.

"It's such an overwhelming positive that people are getting access; the complaints are just noise," observes David Strait of Washington University in St. Louis. He notes that in 2000, White wrote a prominent editorial in which he asserted that, given the intense public interest in human origins, paleoanthropologists have a special duty to get things right. "That's completely wrong," Strait asserts. "Of course, we should try to do things well, but science should operate by falsifying possibilities. We narrow down the possible truths to get a better idea of what happened in the past, and there is always the possibility for new data to emerge that change everyone's thinking." By making the fossils available to other researchers, Strait says, Berger has given those scientists who disagree with him an avenue to test their ideas against his: "The field moves forward only if people can study the stuff."

In the meantime, with or without the opposition's approval, work will continue apace at Rising Star. The geologists are reconstructing the history of the cave, the excavators are recovering more fossils from the chamber, the molecular biologists will attempt to extract DNA from the bones. And the fossil hunters are seeking new leads. "[*H. naledi*] should launch the greatest age of exploration there ever was," Berger declares with characteristic zeal. If it doesn't, maybe the team's next find will: he reveals that his explorers have already made progress on that front. Pressed for more detail, Berger demurs, other than to say with a sly grin that they have located "more than one" new site that has set his heart to racing like Rising Star did when he first saw those grainy photographs. The show will go on. SA

Kate Wong is a senior editor at *Scientific American.*

MORE TO EXPLORE

Geological and Taphonomic Context for the New Hominin Species *Homo naledi* from the Dinaledi Chamber, South Africa. Paul H.G.M. Dirks et al. in eLife, Article No. 09561. Published online September 10, 2015.

***Homo naledi*, a New Species of the Genus *Homo* from the Dinaledi Chamber, South Africa.** Lee R. Berger et al. in eLife, Article No. 09560. Published online September 10, 2015.

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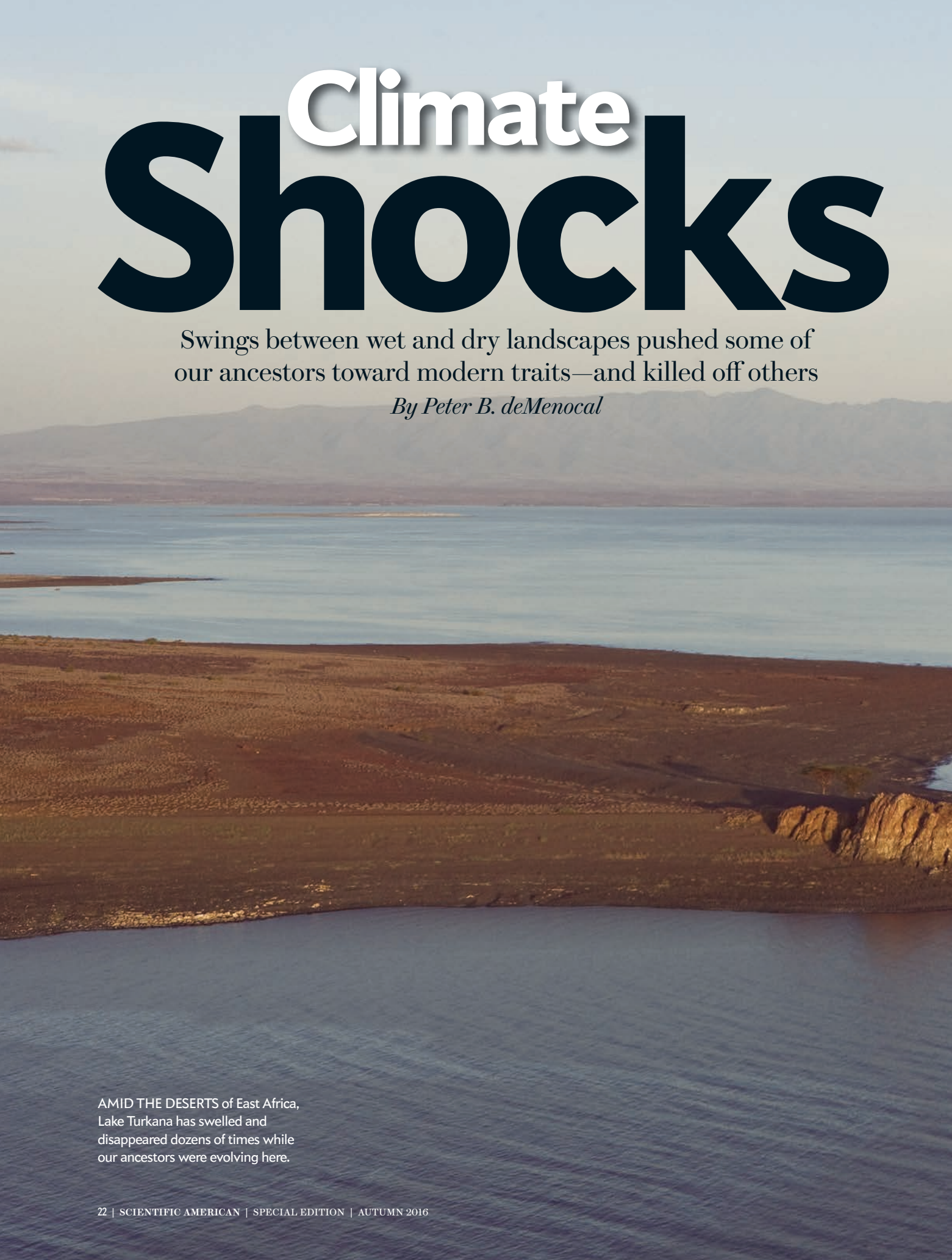
Climate Shocks

Swings between wet and dry landscapes pushed some of our ancestors toward modern traits—and killed off others

By Peter B. deMenocal



AMID THE DESERTS of East Africa, Lake Turkana has swelled and disappeared dozens of times while our ancestors were evolving here.

SCRAMBLING UP THE STEEP BANK OF A SMALL WADI, OR GULLY, NEAR THE western shore of Lake Turkana in northern Kenya, I stop on a little knoll that offers a view across the vast, mostly barren desert landscape. The glittering, jade-blue lake contrasts in every way with the red-brown landscape around it. This long, narrow desert sea, nestled within Africa's Great Rift Valley, owes its existence to the Omo River, whose winding flow delivers runoff that comes from summer monsoon rains in the Ethiopian highlands, hundreds of miles north.

The heat here has to be respected. By noon it feels like a blast furnace. The sun beats down, and the hot, stony ground fires it back upward. Scanning the dusty horizon, with the lake winking in the distance, I find it hard to imagine this place as anything but a desert.

Yet evidence for much wetter times is everywhere. Indeed, the little hillock under my boots is a thick chunk of ancient lake sediments that date back 3.6 million years, when a much larger and deeper Lake Turkana filled this basin to the brim. The glassy remains of fossil lake algae make up white, sandy layers, and large fish fossils are common. At times in the past, this rocky desert was carpeted with grasslands and trees and lakes.

Such climate changes may have played a big role in shaping human evolution, a growing number of scientists believe. The Lake Turkana region, together with other sites in East and South Africa, possesses most of the fossil record of early human origins and our evolutionary journey since our lineage split from African apes more than seven million years ago.

Remarkably, major shifts in African climate coincide with two moments on that ancestral path, roughly a million years apart, that mark significant changes in our family tree. The first evolutionary shake-up happened between 2.9 million and 2.4 million years ago. The famous ancestral lineage of "Lucy" and her ilk (*Australopithecus afarensis*) became extinct, and two other, quite distinctive groups appeared. One of them had the hints of some modern-looking traits, including larger brains. Their owners were the very first members of our own genus, *Homo*. Crude stone tools appeared near these fossils. The other group besides *Homo* that emerged at this time looked different: a stoutly built, heavy-jawed and ultimately unsuccessful lineage known collectively as *Paranthropus*.

The second shake-up occurred between 1.9 million and 1.6 million years ago. An even larger-brained and more carnivorous species, *Homo erectus* (called *Homo ergaster* by some scientists), appeared on the scene. Its taller, more lithe skeleton was nearly indistinguishable from that of modern humans. This species was also the first to leave Africa to populate Southeast Asia and Europe. Stone tool technology also got a major upgrade: the first hand axes showed up, with large blades carefully shaped on two sides.

Why were these evolutionary milestones, harbingers of modern humanity, so clustered in time? A number of scientists now think two episodes of climate change may have been the cause. These two ecological jolts, coming after long periods of extremely gradual change, moved the cradle of humanity toward increasingly dry and open grasslands. While these broader shifts were happening, the climate whipsawed rapidly between wet and dry periods, so to thrive, our ancestors had to adapt to rapidly changing landscapes.

The evidence comes from an array of new data that tell us how and why African climate and vegetation changed during these big human evolutionary moments. Scientists are now able to extract and analyze molecular remnants of ancient African vegetation from layers of sediments such as the ones I stood on. Chemical analyses of our ancestors' teeth reveal what they ate as the landscape changed. The creatures that adapted to these shifts—those that showed flexibility in what they ate and where they lived—appear to be the ones that prospered. This emphasis on flexibility in the face of new environmental challenges seems to be a trait that carries forward in the human lineage. Other forebears, who did not appear to change with the times, died out. Rick Potts, a paleoanthropologist at the Smithsonian Institution, calls the role of flexibility in making us what we are "variability selection."

LIFE SHAPED BY CLIMATE

THEORIES LINKING CLIMATE CHANGE and evolution go back to Charles Darwin. His premise was that large-scale shifts in climate can shake up the kinds of food, shelter and other resources available in a given region. The disappearance of a favorite food or the replacement of a long wet season with a longer dry one create pressures that lead, eventually, to adaptation, extinction or evolution into different species. The environment, set by climate, will favor creatures with genes for certain advantageous traits, such as larger brains. Over time, those creatures and the genes they carry will come to dominate because more of them will survive. In *On the Origin of Species,* Darwin noted that seasons of extreme cold or drought were effective checks on species numbers.

This process of change is not always subtle or gentle. Each of the "big five" mass extinctions in the fossil record of life on earth during the past 540 million years was accompanied by an environmental disruption. During each of these events, between 50 and 90 percent of all species perished, but this was followed by bursts of new, very different species. These episodes define the major chapters in the history book of life, when new biotic worlds emerged and flourished. We mammals owe a debt of gratitude to the Manhattan-size meteorite that struck the Yucatán Peninsula in what is now Mexico about 66 million years ago. It killed off the dinosaurs (and numerous other less charismatic species), ushering in the rapid radiation and diversification of mammals.

One group of those mammals led, after many more branchings and a lot of time, to us. For these hominins (modern humans and our extinct relatives), scientists have tried out several ideas about the way the environment shaped evolution. The "savanna hypothesis" was one. In its earliest incarnation, scientists proposed that our early human ancestors, with burgeoning bipedality, large brains and toolmaking, were better suited to rapidly expanding savanna grasslands, where competition for resources was fiercer, and they left our apelike forebears behind in receding forests.

IN BRIEF

Changes in climate are emerging as elements that shaped human evolution over millions of years, as scientists learn that such alteration coincided with the extinction of some of our ancestors and the success of others.

Evidence from ancient soils in East Africa, deep-sea sediments and fossil teeth from our forerunners combines to reveal rapid swings between wet and dry environments, as well as two distinct periods when grasslands replaced more wooded areas.

The emergence of our own genus, *Homo,* our varied diet, advances in stone tool technology and the very human trait of adaptability in the face of ongoing change may be tied to these episodes, according to one theory.

PRECEDING PAGES: MICHAEL POLIZA *National Geographic Creative*

1

2

STONE AGE EATING: A distant ancestor, *Paranthropus boisei* (*1*), lived in open plains and mostly ate grasses or related foods, as indicated by chemical analysis of fossil teeth. But *Homo erectus*, sometimes called *Homo ergaster* (*2*), a member of our own genus that lived in the same landscape, had a more varied diet, and adaptability may have helped its evolutionary success.

This dated view, which still shows up in some textbooks, is incorrect. There was no one-time habitat switch from forests to grasslands but rather a rapid succession of wet-dry cycles that moved, in distinct steps, toward drier conditions. Also, we did not acquire human traits in one single moment but rather in a series of concentrated bursts just when the environment was shifting.

WET AND DRY CYCLES

EVIDENCE FOR THESE BURSTS of landscape change and evolution comes not just from land but from the sea. African ground sediments are often hard to analyze because of erosion and other geologic disturbances. In the deep oceans, however, they remain undisturbed. By drilling into the seafloor near the African coasts, geologists like myself have been able to penetrate a multimillion-year time capsule, recovering long cores of sediments that preserve complete records of past African environments. To get these cores, we need a special ship. That is why a team of 27 scientists and I spent two months in the fall of 1987 on the 470-foot drilling vessel *JOIDES Resolution*.

"Core on deck!" the driller over the PA system would squawk in his Texan twang. We scientists groaned, donned our hard hats, and marched out of the ship's cool, comfortable laboratories into the blinding Arabian sun to carry yet another 30-foot segment of deep-sea sediment core inside for analysis. The *Resolution* is an internationally funded research ship designed to explore and drill the ocean bottom and recover the earth's history recorded there. We were drilling through layers of deep-sea sediment in the Arabian Sea in a mile and a half of water, taking cores from nearly half a mile into the sea bottom. Since the divergence of great ape and human lineages several million years ago, the ocean bottom here had accumulated nearly 1,000 feet of deep-sea mud in the dark, peaceful abyss, at a rate of about one and a half inches every 1,000 years.

The sediments here consist of mixtures of fine-white calcium carbonate fossil shells from ancient ocean plankton and darker, silty grains of dirt blown from areas of Africa and Arabia by windy monsoons. When the mix looks darker and gritty, it indicates drier, dustier times. When it looks lighter, that reflects wetter, more humid conditions.

Laying the split sediment core on a table inside the ship's spacious research labs, we could see that the alternating light and dark layers repeated every three feet, more or less, which meant they changed about every 23,000 years. It was clear that African climate history had been one of continuous swings between wetter and drier times. That was nothing like a single, sharp shift to a savanna.

These swings reflected the known sensitivity of African and Asian monsoonal climates to the earth's orbital wobble, which occurs as a regular 23,000-year cycle. The wobble changes the amount of sunlight hitting our planet in a given season. For North Africa and South Asia, more or less heat during the summer increased or decreased monsoon rainfall, making these regions either much wetter or drier as our planet wobbled back and forth.

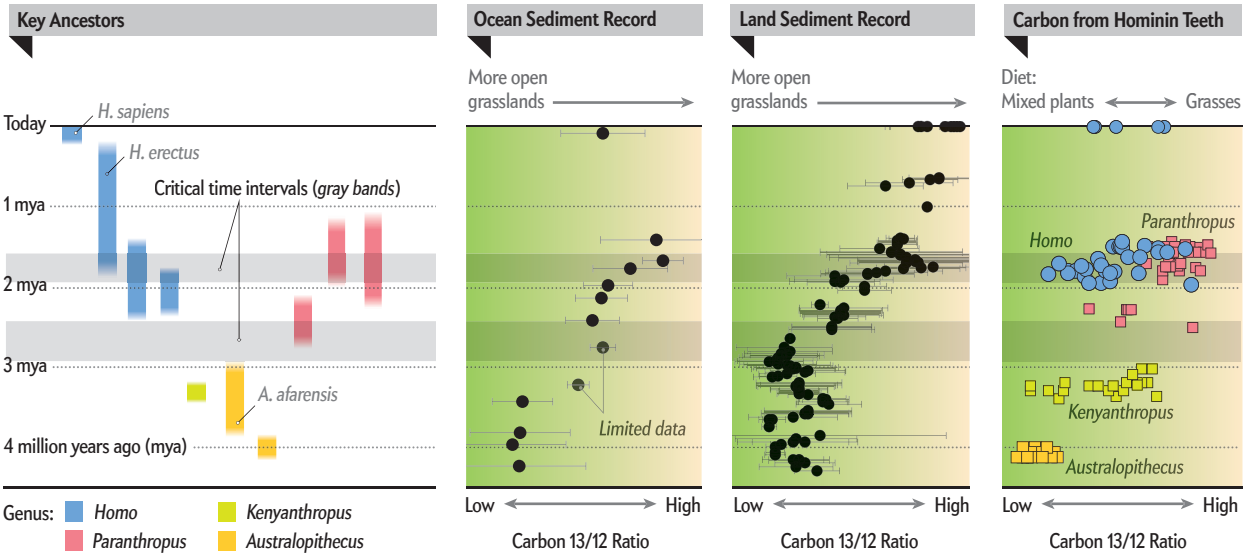
Just how wet things got is recorded in magnificent rock art drawn between 10,000 and 5,000 years ago by humans during the most recent wet period in North Africa. Art found across the Sahara depicts lush landscapes filled with elephants, hippopotamuses, giraffes, crocodiles and bands of hunters chasing gazelles. The Sahara was covered with grass and trees; lake basins, now overrun by sand dunes, were filled to the brim with water. A swollen Nile River rushed into the eastern Mediterranean, and black, organic-rich sediments called sapropels accumulated on the Mediterranean seafloor. They alternated with whiter layers laid down during dry periods, a bar-code message telling of African climate cycles reaching deep into the past, just like the changing dust layers recovered from the Arabian Sea.

RECONSTRUCTION AND PHOTOGRAPH © 2014 JOHN GURCHE (1); FROM *SHAPING HUMANITY*, BY JOHN GURCHE, YALE UNIVERSITY PRESS, 2013 (2)

FINDINGS

A Climate for Change

Two moments in our evolutionary history show a tantalizing connection between climate swings and the life and death of key members of our family tree. Starting just after three million years ago, the species *Australopithecus afarensis* vanished, and the groups *Paranthropus* and *Homo* (our own genus) appeared. During this period, changes in carbon isotope ratios from land and ocean sediments show that dry grasslands rapidly expanded and wetter woodlands shrank. Starting after two million years ago, *Homo erectus,* one of our direct ancestors, appeared and migrated out of Africa. Again, the carbon evidence shows grasslands got another boost. Yet carbon in the teeth from *H. erectus* indicates the consumption of a mixed diet and an ability to find food from a variety of sources even as grasslands enlarged. *Paranthropus* teeth, however, showed the group (like an earlier extinct forebear, *Kenyanthropus*) was restricted to eating from grassy surroundings.



THE LAST OF LUCY

SUPERIMPOSED ON THESE orbital wet-dry cycles were larger steps toward dry and open grasslands. Small patches of grasslands first expanded in East Africa nearly eight million years ago. But vast grassy plains such as the Serengeti were only established permanently after three million years ago. Just about this time, our evolutionary history was given a jolt as well.

We lost Lucy. Her extremely successful species, *A. afarensis,* had survived in East Africa for 900,000 years, starting at about 3.9 million years ago. But just under three million years ago, Lucy's kind disappeared from the fossil record.

Next the *Paranthropus* group appeared, followed 2.6 million years ago by the first signs of stone choppers and scrapers and then in a few hundred thousand years by early *Homo* fossils.

We know these changes in our family tree and in technological invention happened during a shift in overall climate because of some clever scientific detective work, tracing the fingerprints left by some plants that flourished in wetter environments and others that thrived in drier times.

Savannas are open tropical ecosystems composed of grasses and sedges, sometimes spotted with clusters of woody trees. Savanna grasses do very well in hot, dry regions because, to take up carbon from the atmosphere, they use a specific photosynthetic pathway called C4. This set of reactions is miserly with carbon and water, an adaptation to life in dry and low-CO_2 environments. Woody vegetation such as trees finds homes in wetter ecosystems because it uses another photosynthetic pathway called C3, which requires much more water.

Thure E. Cerling and his colleagues at the University of Utah developed a way to reconstruct the vegetation history of ancient landscapes. Some years ago researchers discovered that C4 grasses have a greater abundance of the heavier but rarer carbon 13 isotope relative to the lighter, more abundant carbon 12 isotope. But C3 shrubs and woody plants have a lower carbon 13/12 ratio. The scientists discovered that they could take samples of soil or nodules of rock from a given landscape, analyze the carbon ratios, and use them to accurately estimate the percentage of C4 grasses versus C3 woody plants that were once in that area.

When they looked at the East African sediment from sites that had yielded fossil hominins, the researchers learned that East African landscapes were predominantly C3 forest and shrublands before eight million years ago. After that, the proportion of C4 grasslands increased gradually. Then a relatively large and fast shift occurred between three million and two million years ago.

During this shift, grasslands expanded rapidly across present-day Kenya, Ethiopia and Tanzania. The spread was accompanied by a rise in the proportion of grazing mammals, shown by their abundant fossils. As time ticked forward, closer to two million years ago, African antelopes—their horns, whose different shapes indicate different species, are well preserved—seem to have undergone extensive speciation, extinction and adaptation, rather like our hominin forebears.

SOURCE: PETER B. DEMENOCAL

Bovids, the family to which these even-toed ungulates belong, represent roughly one third of all African fossils. Thus, they provide a much larger data set than do the much scarcer hominins. Paleontologist Elisabeth Vrba of Yale University conducted an all-Africa analysis of bovid evolution spanning the past six million years. Her study identified specific times when rates of bovid speciation and extinction were well above normal background levels. The two largest of these events occurred near 2.8 million and 1.8 million years ago, coinciding with the periods of grassland growth that geologists observe, although recent work by René Bobe, now at Gteorge Washington University, and Anna K. Behrensmeyer of the Smithsonian Institution suggests these events may be more muted. The anatomy of these fossils hints that some of them were taking advantage of the landscape change. For example, many new grazing bovid species appeared with specialized molars for chewing the abrasive, grassy diet.

DIETS AND LANDSCAPES

AS WAS THE CASE FOR BOVIDS, this vegetation change most likely had a profound effect on our own ancestors because we do not just live in an environment—we eat it. Paleo diet research turns out to be quite useful for understanding how hominins were affected by changing landscapes. Just as isotopes in soils can be used to infer the relative abundance of grasslands in an ancient landscape, scientists have recently started to analyze the isotopic composition in our forerunners' fossil teeth. The carbon isotope analysis of a tooth from a modern American would sit squarely on the C4-grass side of the scale because much of what we consume—meat from cows, soft drinks, snacks, sweets—derives from corn, a C4 grass.

Prehistoric diet changes seem to be part of that second big evolutionary moment in our history, nearly two million years ago, when *Homo* fossils that looked more modern first appeared. Cerling and his many colleagues have been examining the teeth of Turkana Basin fossils. A few years ago they published a remarkable study that showed a dietary split between early members of our own genus, *Homo,* and members of the heavy-jawed *Paranthropus* group, at just under that two-million-year mark. One species, *Paranthropus boisei,* has sometimes been called Nutcracker Man because of its impressively large molars and massive jawbones. The carbon isotope tooth data from this species indicate it indeed ate a narrow, mostly C4-based diet. Fine microscopic scratches on the teeth, however, suggest it was not cracking nuts at all but rather eating soft C4 grasses and sedges.

The big surprise was for *Homo*. These early teeth recorded a diet that bucked the landscape trend toward greater C4 grass cover. The tooth isotopic data for early *Homo* indicate a strikingly mixed, roughly 65–35 diet of C3- and C4-based foods. It shows that *Homo* sought diverse foods from a landscape that was becoming increasingly uniform. Early *Homo* had a varied, flexible diet and passed its genes to subsequent lineages, eventually leading to us. *Paranthropus,* in contrast, lived in a narrow C4 dietary niche and eventually became extinct.

It is tempting to speculate that the more complex stone tools that appeared with this group of *Homo*—hand axes, cleavers and the like, tools that required more effort to fashion and could be put to multiple uses—were better suited to help their owners exploit varying food sources. We are still not at all sure what these organisms were eating, but we do know which dietary adaptations were ultimately successful.

FILLING IN THE CLIMATE GAPS

THIS C3/C4 STORY, though intriguing, has some holes in it: in particular, gaps of several thousands of years in land sediment sequences. But again, the ocean sediments and their more complete records can help fill in the blanks. A very promising technique for continuously tracking vegetation changes has emerged in the past decade. All terrestrial plants have waxy leaf coatings that protect them from injury and dehydration. When plants die or become abraded, the waxy coatings are carried by the winds, along with mineral dust and other particles. These coatings are made out of tough little molecules, long carbon-based chains known as lipids. They are resistant to degradation and possess the carbon isotopic signature from their host plant type, C3 or C4. Once chemically isolated from sediments, these plant wax lipids can be measured and their carbon signature determined as C3 or C4. The relative abundance of a particular type lets us estimate the amounts of grass versus trees and scrubs on ancient landscapes.

Sarah J. Feakins, now at the University of Southern California, and her colleagues applied this technique to reconstruct hominin environments. Analyzing sediments from a drilling site in the Gulf of Aden, she confirmed that East African grasslands expanded between three million and two million years ago, perhaps by as much as 50 percent. Feakins also found that these plant wax biomarkers varied within the dust layers that marked the short-term swings driven by orbital cycles and monsoons. The grasses and woodlands shifted back and forth on this shorter scale, and many of these swings were nearly as large as the long-term shift to more open, grassy landscapes. At the famous fossil site Olduvai Gorge in Tanzania, where hominins lived 1.9 million years ago, scientists Clayton R. Magill and Katherine H. Freeman, both then at Pennsylvania State University, found similar biomarker shifts.

We are closing in on a clearer picture of the how and why of human origins. Gone is the old image of our ancestors emerging from some ancient dark forest to assert dominion over the grassy plains. In its place is new evidence for a series of rapid climate cycles and two large shifts that established the African savanna we know today. Some evidence indicates that our most successful forebears had the flexibility to adapt to these changes. Researchers are already trying to firm up this connection between climate and these evolutionary events with more detailed investigations. Still, it appears as if an answer to the age-old question "How did I get here?" is no longer beyond our reach. SA

Peter B. deMenocal is a professor in the department of earth and environmental sciences at the Lamont-Doherty Earth Observatory at Columbia University. He was a co-author of the National Research Council's report *Understanding Climate's Influence on Human Evolution.*

MORE TO EXPLORE

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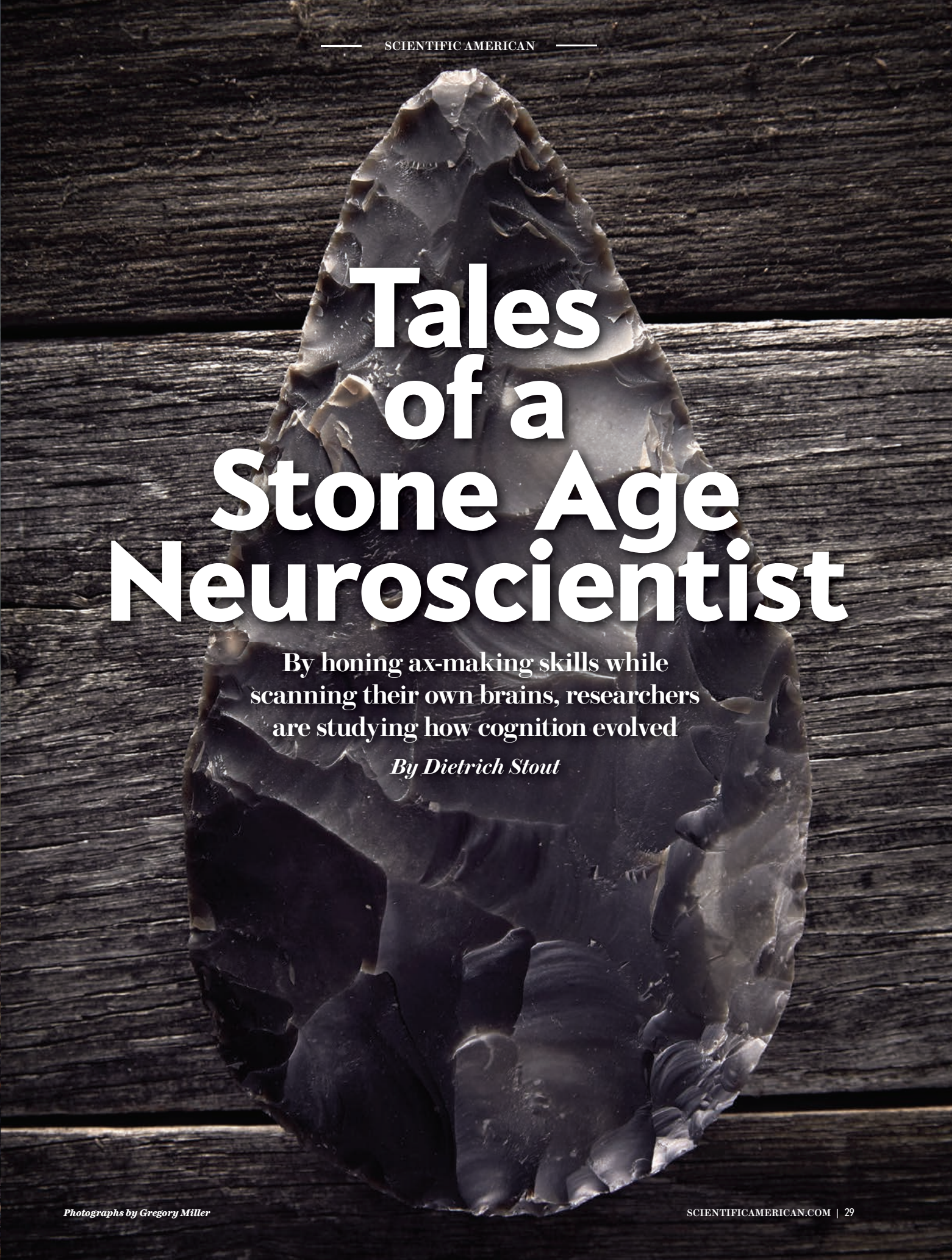
scientificamerican.com/magazine/sa

TOOLMAKER: Anthropology professor Dietrich Stout works on a stone tool at Emory University's Paleolithic Technology Laboratory.



Tales of a Stone Age Neuroscientist

By honing ax-making skills while scanning their own brains, researchers are studying how cognition evolved

By Dietrich Stout

Photographs by Gregory Miller

I STILL HAVE THE FIRST STONE HAND AX I EVER MADE. IT'S A PRETTY POOR SPECIMEN, crudely chipped from a piece of frost-fractured flint I picked up on a walk through a farmer's field in West Sussex, England. It would not have impressed the human ancestors known to us as *Homo heidelbergensis*. These cousins of *Homo sapiens* from 500,000 years ago left much nicer hand axes at a nearby archaeological site in Boxgrove. Still, I worked hard at making this simple cutting tool, and I am proud of it. What really matters, though, is not that I am dabbling in a new hobby. What matters is that my dabbling was intended to probe key questions of human evolution and the emergence of language and culture that are hallmarks of our species.

Replicating the skills of prehistoric peoples to understand human origins is not unprecedented—archaeologists have done it for decades. In the past 15 years, however, we have taken this approach in exciting new directions.

Working together, archaeologists and neuroscientists have brought brain-scanning machines to bear in observing what happens underneath the skull when a modern-day toolmaker chips away patiently at a stone, shaping it into a hand ax. With this view into the brain, we hope to identify which regions within may have evolved to help Paleolithic peoples chisel a well-crafted ax or knife from a formless hunk of rock.

These collaborations between archaeologists and neuroscientists have revived a largely discredited idea: that toolmaking was an important driver of the evolution of humans. British anthropologist Kenneth Oakley asserted 70 years ago in his influential book *Man the Tool-maker* that toolmaking was the "chief biological characteristic" of humanity that drove the evolution of our "powers of mental and bodily co-ordination."

The idea fell out of favor as behavioral scientists documented tool use and even toolmaking in nonhuman species such as apes, crows, dolphins and octopi. As paleontologist Louis Leakey put it in his now famous reply in 1960 to Jane Goodall's historic first report of chimpanzee tool use: "Now we must redefine tool, redefine Man, or accept chimpanzees as humans." For many scientists, complex social relationships replaced toolmaking as the central factor in primate brain evolution. In the 1980s and 1990s influential "Machiavellian intelligence" and "social brain" hypotheses argued that the greatest mental challenges primates face are in outsmarting other members of their own species, not in mastering their physical environment. These hypotheses gained empirical support from the observation that primate species that form large social groups also tend to have large brain sizes.

But more recent work, including our own, has shown that the "Man the Tool-maker" idea is not dead (although Oakley's language is clearly outdated). Toolmaking need not be unique to humans to have been important in our evolution. What matters is the kind of tools we make and how we learn to make

IN BRIEF

One way to answer questions about human evolution—and, in particular, the development of language and culture—entails replicating the skills used by prehistoric peoples.

A high-tech version of this approach uses brain-scanning machines to observe what neural regions become active when a toolmaker chips away at stone being shaped into a hand ax.

Crossover collaborations between archaeologists and neuroscientists have revived the largely discredited idea that the act of toolmaking served as a key driver of human evolution.

Teaching and learning the art of Stone Age toolmaking may, in fact, have posed a formidable enough challenge to our ancestors that it spurred the evolution of human language.

KNAPPING CLASS: Nada Khreisheh (*1, far right*) teaches hand-ax toolmaking 20 hours a week in the outdoor work area at Emory's Paleolithic Technology Laboratory. Each student receives a total of 100 hours of instruction. The flint hand ax (*2*) was the first such tool made by the author.

them. Among primates, humans truly stand out in their ability to learn from one another. They are particularly adept at imitating what another person does. Mimicry is a prerequisite for learning complex technical skills and is thought to underlie the stunning ability of human culture to accumulate knowledge in a way that other apes do not. So it seems premature to abandon the idea that ancient stone tools might provide important information about human cognitive evolution. Teaching and learning increasingly complex toolmaking may even have posed a formidable enough challenge to our human ancestors that it spurred evolution of human language. In fact, many neuroscientists now believe that linguistic and manual skills both rely on some of the same brain structures.

To test these ideas, we have had to analyze carefully how ancient tools were made and compare these findings with evidence of the way relevant brain systems evolved. In studying these questions, we ran into immediate difficulties because neither brains nor behaviors appear in the fossil record. Given the paucity of evidence, our only recourse was to simulate in a laboratory setting the types of skills that were passed from generation to generation many millennia ago. For this reason, my students, collaborators and I have spent many years trying to emulate the skills of Paleolithic toolmakers.

EXPERIMENTAL ARCHAEOLOGY

USING MODERN BRAIN-SCANNING techniques to study some of humanity's oldest technologies may seem strange. We did get some funny looks when we first started wheeling carts of rocks into a state-of-the-art neuroimaging lab. But there is nothing startling about archaeologists performing experiments. Studying the present has long been one of the most important methods for understanding the past. Scientists have devised experiments to replicate ancient smelting techniques (archaeometallurgy) and to observe the relentless decay of animal carcasses (taphonomy)

to better understand how they fossilize. Casual experiments in stone toolmaking—"knapping," as archaeologists call it—date back to the 19th century, and more controlled experiments are now well established in the study of lithic technology.

The scope of these experiments has grown in recent years. My graduate advisers—Nicholas Toth and Kathy Schick, both now at Indiana University Bloomington and the Stone Age Institute—proposed in 1990 using a then newly developed imaging technique to investigate what happens in the brain when making a Paleolithic tool. Following up on this initial idea during the past 15 years, I have made a major goal of my own research to figure out what happens inside the brain when a person knaps away at a piece of stone.

My lab now functions as something of an apprenticeship program in stone toolmaking. As I write, I can hear the tick, tick, tick of novice knappers adding yet more chips to a pile of broken flint in the work area outside my office at Emory University. Last year that pile reached 10 feet across, measured five inches in height and contained more than 3,000 pounds of shattered rock. I watch through a window as postdoctoral researcher Nada Khreisheh leans over to offer advice to a frustrated student.

Khreisheh currently spends about 20 hours a week training 20 students (each receives 100 hours of instruction) in the ancient art of hand-ax-making. This is our most ambitious project to date. Every training session is video-recorded so we are able to later analyze which learning techniques work best. We collect and measure each finished artifact to track skill development. The students must undergo repeated magnetic resonance imaging to examine changing brain structure and function, as well as psychological tests to see if particular abilities, such as planning or short-term memory, may be linked to toolmaking aptitude. It is a huge amount of work but essential to understanding the subtleties of this prehistoric technology.

THE NEOPHYTE MUST MASTER A PERCUSSIVE TECHNOLOGY SO DEMANDING THAT A SMALL ERROR CAN COMPROMISE THE ENTIRE WORKPIECE.

If nothing else, all this effort has taught us that making these tools is difficult. But what we want to know is why it is so hard. Oakley and other proponents of the "Man the Tool-maker" argument thought the key to toolmaking was a "uniquely human" ability for abstract thought—that is, the ability to imagine different kinds of tools as a kind of mental template to be reproduced. I respectfully disagree. As any experienced craftsperson might tell you, knowing what you want to make is not the hard part. The difficulty lies in actually making it.

Knapping a hand ax requires the neophyte craftsperson to master a percussive technology that involves using a handheld "hammer" of stone, bone or antler to chip flakes off a stone, shaping it into a useful tool. The work requires powerful blows, accurate to within a few fractions of an inch, which are delivered too rapidly to allow for a midswing correction. Like chiseling a marble sculpture, each strike removes something that cannot be put back. Even small errors can compromise the entire workpiece.

Using a motion-tracking system, movement scientist Blandine Bril and her colleagues at the School for Advanced Studies in the Social Sciences in Paris have shown that, unlike novices, experienced knappers adjust the force of their blows to produce flakes of different sizes. Stringing together a series of such blows to achieve an abstract design goal such as a hand ax is achievable only after acquiring the necessary control through long and painstaking practice.

Our ancestors faced the same challenges when they learned to make stone tools, and their lives probably depended on success in doing so. The demands of toolmaking—combined with complex social interactions for teaching these skills—may have become driving forces for human cognitive evolution. We have labeled this modern reboot of Oakley's "Man the Tool-maker" hypothesis as *Homo artifex*—the Latin word *artifex* signifying skill, creativity and craftsmanship.

TOOLS ON THE BRAIN

TEACHING STUDENTS to work stone is not the only technical challenge in learning about prehistoric practices. Standard brain imaging does not lend itself to certain aspects of studying stone toolmaking. If you have ever had a scan in a MRI machine, you probably remember being told emphatically not to move because it would ruin the image. Unfortunately, lying motionless inside a two-foot-wide tube is not conducive to knapping, although you might be tempted to nap.

In our early experiments, we circumvented this problem by using a brain-imaging technique known as FDG-PET (fluorodeoxyglucose positron-emission tomography). The intravenous line to supply the radioactive molecule used in PET to image brain activity needs to be injected into the foot to allow knappers to use their hands, a somewhat painful procedure. The test subject can then freely chip away at the chunk of stone destined to become an ax or knife while the tracer is taken up in metabolically active tissues in the brain. After the subject is finished, we run a scan to determine where in the brain the chemical has accumulated.

Using this technique, I set out to investigate two Stone Age technologies—Oldowan and Late Acheulean—that bracket the beginning and end of the Lower Paleolithic, a critical evolutionary period from 2.6 million to 200,000 years ago when the brains of hominins (humans and their extinct ancestors) nearly tripled in size. The question we wanted to explore in my lab was whether the development of these technologies placed new demands on the brain that, over the millennia, might have led through natural selection to its expansion.

Oldowan toolmaking (named after Tanzania's Olduvai Gorge, where it was first described in the mid-20th century by paleoanthropologist-archaeologist team Louis and Mary Leakey) involves striking sharp flakes from a cobble core. These simple flakes of rock became humanity's first "knives." Conceptually, toolmaking does not get much simpler. But our early PET data confirmed that the actual knapping process still remains a demanding task that goes far beyond just simply striking rocks together.

In our study, we allowed participants to practice for four hours without any instruction. As they became familiar with the task, they learned to identify and pay attention to particular features of the core, focusing, for instance, on areas that stuck out and would be easier to break. This learning is actually reflected in different patterns of activity in the visual cortex at the back of the brain before and after practice. But four hours' practice is not very long,

even for humanity's earliest technology.

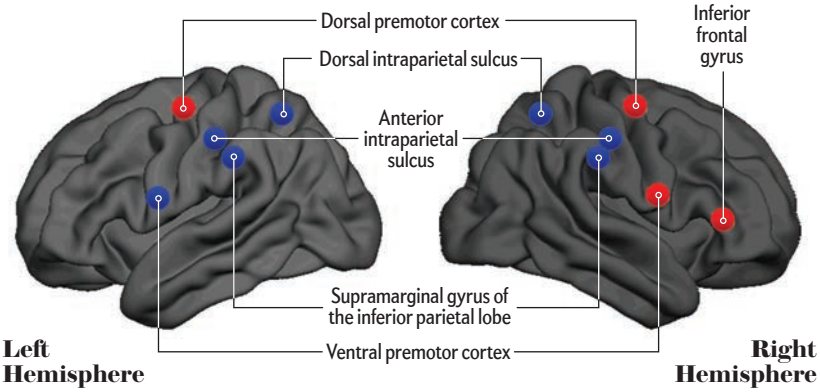
In truly experienced knappers, who can approximate the documented skills of real Oldowan toolmakers, something different is seen. As shown by Bril and her colleagues, experienced toolmakers distinguish themselves by their ability to control the amount of force applied during the percussive strike to detach flakes efficiently from the core. In the experts' brain, this skill spurred increased activity in the supramarginal gyrus in the parietal lobe, which is involved in awareness of the body's location in its spatial environment.

About 1.7 million years ago flake-based Oldowan technology began to be replaced by Acheulean technology (named after Saint-Acheul in France), which involved the making of more sophisticated tools, such as teardrop-shaped hand axes. Some Late Acheulean hand axes—those from the English site of Boxgrove that date back 500,000 years, for instance—were very finely shaped, with thin cross sections, three-dimensional symmetry and sharp, regular edges, all indicating a high level of knapping skill.

IMAGING

An Expansion of Brainpower

Scanning techniques reveal how more of the brain gets used as toolmaking becomes more sophisticated. Imaging distinguished areas activated when a modern toolmaker crafted an implement reminiscent of simple Oldowan tools (2.6 million to 1.6 million years ago) compared with regions active when making Acheulean hand axes (1.6 million to 200,000 years ago). Blue dots denote brain regions utilized when chiseling both Oldowan and Acheulean tools; red ones lit up as well when knapping an Acheulean hand ax.



Modern knappers know that this technique requires not only precise control but carefully reasoned planning. Like a golfer selecting the right club, knappers use a variety of "hard" (stone) and "soft" (antler/bone) hammers as they work through planned flaking sequences that prepare core edges and surfaces to fracture in the desired pattern. They must switch back and forth between different subtasks while keeping the overall goal of a finished ax firmly in mind, resisting the temptation to take shortcuts. I know from bitter experience that you can't cheat the physics of stone fracture. It is better to just quit for the day when you are tired or frustrated.

The demands of knapping a Late Acheulean tool also produce a characteristic signature in the brain scanner. Some of the same areas are involved in both Oldowan and Acheulean knapping. But our Acheulean PET data also show activation extending into a specific region of the prefrontal cortex, called the right inferior frontal gyrus. Decades of research by neuroscientists such as Adam Aron of the University of California, San Diego, have linked this region to the cognitive control needed to switch between different tasks and to hold back inappropriate responses.

We have since corroborated our PET results by using MRI, which provides higher-resolution imaging. To do this, we had to figure out a way to keep subjects immobilized. Working with social neuroscientist Thierry Chaminade, now at the Institute of Neurosciences of Timone at Aix-Marseille University in France, I asked subjects to lie still in the scanner and watch knapping videos rather than actually trying to make tools. This approach works because, as Chaminade and others have shown, we use many of the same brain systems to understand observed actions as we do to execute them. Despite different methodologies, we found the same responses in the brain's visuomotor areas for both Oldowan and Acheulean knapping—and increased activity in the right inferior frontal gyrus when subjects watched the crafting of Late Acheulean tools.

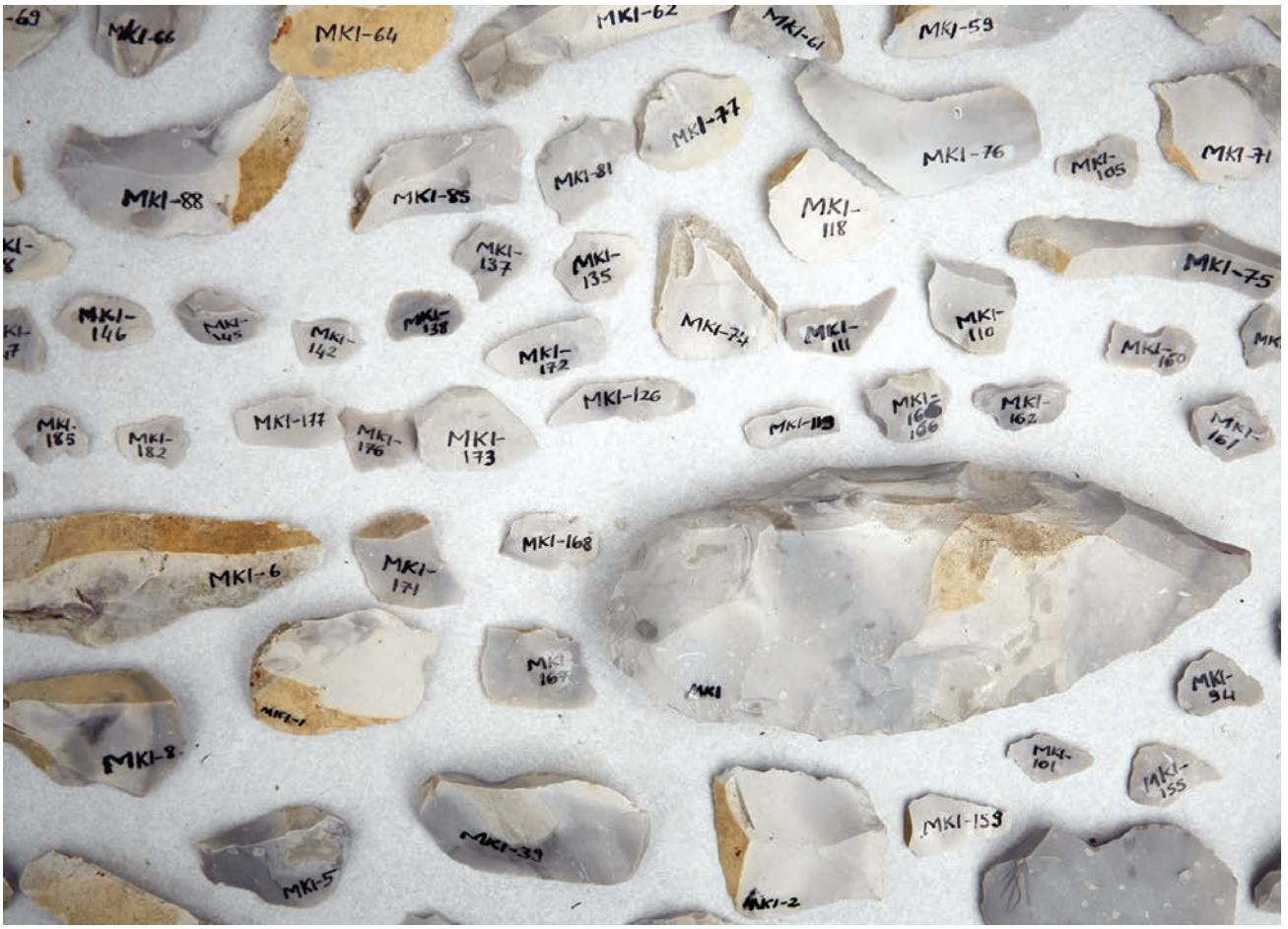
We concluded that the ability to learn demanding physical skills would have been important to early Oldowan stages of human technological evolution but that Acheulean methods also required an enhanced level of cognitive control furnished by the prefrontal cortex. In fact, this observation agreed fairly well with the fossil evidence, which shows that some of the fastest increases in brain size over the past two million years occurred during the Late Acheulean. But that discovery did not establish which event was a cause and which was a consequence. Did toolmaking actually drive brain evolution in *H. artifex,* or did it simply come along for the ride? To tackle this question, we needed to get even more serious about studying how the brain learns to make tools.

LEARNING AND EVOLUTION

IT TOOK ME about 300 hours of practice to equal the skills of the Late Acheulean toolmakers at Boxgrove. The learning process might have gone quicker if I had worked with a teacher or been part of a toolmaking community. But I am not really certain. Despite decades of experimental knapping, almost no systematic studies of the learning process have been conducted. In 2008 Bruce Bradley, a professor of archaeology at the University of Exeter in England and a longtime experimental knapper, invited me to address that gap in our knowledge. Bradley wanted to train the next generation of British academic knappers, and he thought I might like to collect some neuroimaging data along the way to gain better insight into the learning process. He was right—I did.

One thing that I was particularly excited to try was a relatively new technique called diffusion tensor imaging (DTI), a form of MRI that allows scientists to map the white matter fi-

COURTESY OF THIERRY CHAMINADE *Institute of Neurosciences of Timone, Aix-Marseille University*



CHIPS OFF THE BLOCK: A novice toolmaker knapped a flint hand ax, surrounded here by flakes detached while making the implement. Each piece is labeled, weighed and measured so that the process of learning motor and planning skills can be analyzed in detail.

ber tracts that serve as the brain's "wiring." In 2004 a group led by Bogdan Draganski, then at the University of Regensburg in Germany, used DTI to show structural changes in the brains of volunteers learning to juggle, which challenged the traditional view that the structure of adult brains is relatively fixed.

We suspected that learning to knap would also require some degree of neural rewiring. If so, we wanted to know which circuits were affected. If our idea was correct, we hoped to get a glimpse of whether toolmaking can actually cause, on a small scale, the same type of anatomical changes in an individual that occurred over the course of human evolution.

The answer turned out to be a resounding yes: practice in knapping enhanced white matter tracts connecting the same frontal and parietal regions identified in our PET and MRI studies, including the right inferior frontal gyrus of the prefrontal cortex, a region critical for cognitive control. The extent of these changes could be predicted from the actual number of hours each subject spent practicing—the more someone practiced, the more their white matter changed.

Brain changes—what neuroscientists term "plasticity"—provide raw material for evolutionary change, an effect known as phenotypic accommodation. Plasticity allows species the flexibility to try out new behaviors—to "push the envelope" of their current adaptation. If they happen to discover a good trick, it enters their behavioral repertoire, and the evolutionary race is on: natural selection will favor any variations that enhance the ease, efficiency or reliability of learning the new trick. Our result thus provided important evidence that the idea of *H. artifex* was viable—and that toolmaking *could* actually have driven brain change through known evolutionary mechanisms.

With that information in hand, we needed to know next whether the anatomical responses that we had observed paralleled specific evolutionary developments in the human brain. Fossil skulls cannot provide detailed information about changes to internal brain structures, so we turned to the next best thing: a direct comparison with one of our closest living relatives, the chimpanzee.

Fortunately, I had already enlisted the assistance of Erin Hecht, a recent Emory Ph.D., now at Georgia State University, to assist with the DTI analyses. Hecht's dissertation work comparing chimpanzee and human neuroanatomy had given her access to precisely the data and expertise we needed. The result, published last year, was a DTI-based virtual dissection of white matter tracts in the two species that would identify any differences in the relevant brain circuits. It confirmed what we had suspected: the toolmaking circuits identified in our PET, MRI and DTI

studies were indeed more extensive in humans than in chimps, especially when it came to connections to the right inferior frontal gyrus. This finding became the final link in a chain of inferences from ancient artifacts to behavior, cognition and brain evolution that I had been assembling since my days as a graduate student in the late 1990s. It provides powerful new support for the old idea that Paleolithic toolmaking helped to shape the modern mind. It is far from the end of the story, however.

THROUGH THE KEYHOLE

I LOVE STONE TOOLS, but they provide us with only the narrowest keyhole view of the complex lives of our ancestors. Like a geologist with a seismograph, the trick is to turn these bits of knowledge from the neuroscience of toolmaking into a rich model of Stone Age existence.

Although the evidence from stone tools is limited, we could have done worse. Stone toolmaking takes as much time to learn as many academic skills: a typical American college class is supposed to require about 150 hours of work (10 hours a week over a 15-week semester). In the study with Bradley, trainees logged an average of 167 hours' practice and were still struggling with Acheulean hand-ax-making by the end. Perhaps I should not feel too bad about the 300 hours it took me to learn. But sticking to such a tedious and frustrating practice regimen requires motivation and self-control, both intriguing attributes from an evolutionary perspective.

IMAGING STUDIES HINT THAT NEURAL CIRCUITS USED IN TOOLMAKING WERE CO-OPTED BY THE BRAIN FOR PRIMITIVE FORMS OF COMMUNICATION.

Motivation can come externally from a teacher or internally from the anticipation of a future reward. Many researchers have considered teaching to be the defining feature of human culture, whereas anticipating the future is clearly vital to everything from social relationships to technical problem solving.

Of course, motivational "carrots" take you only so far without the "stick" of self-control. The ability to exercise self-control—the inhibition of counterproductive impulses—is critical to many kinds of cognitive skills. In fact, a recent study led by Evan MacLean of Duke University found self-control and future planning to be correlated with larger brain size across 36 species of birds and mammals. Our own work has now resulted in an accumulation of evidence that ties successful hand-ax-making to brain systems for self-control and future planning—providing a direct link with this comparative evidence of brain-size evolution across species.

Besides demonstrating motivation and self-control, the toolmaker must achieve a depth of understanding about the characteristics of the stone being worked that is very difficult to obtain through self-teaching. The learning curve for knapping follows a staircase pattern: most of the time you just need to practice and consolidate skills, but every once in a while, a bit of advice takes you to the next level. Although it is sometimes possible to discover tricks of the trade of stone toolmaking independently, there is a real advantage to learning from others.

One good way to learn is simply to watch. Although calling someone a good imitator can be taken as an insult, comparative psychologists have come to recognize faithful copying as a pillar of human culture. Work by Andrew Whiten of the University of St. Andrews in Scotland and many others has shown that apes have some ability to imitate but nowhere near the compulsive, high-fidelity copying skills of human children and adults.

Is imitation on its own enough? You might be able to figure out chess by watching enough games, but it would be a lot easier if someone explained the nuances of strategy and tactics. What we want to know is whether this is also true of stone toolmaking and other prehistoric skills. Thomas Morgan of the University of California, Berkeley, and his colleagues recently conducted a stone-toolmaking experiment to examine how knowledge passes from one person to the next. They showed a significant learning advantage when teaching used language instead of simply demonstrating a skill. Further experiments along these lines might one day help answer the great mystery of when and why human language evolved.

Teaching is not the only possible connection between toolmaking and language. Neuroscientists recognize that most regions of the human brain perform basic computations related to a variety of different behaviors. Take, for instance, 19th-century anthropologist Paul Broca's classic "speech" area in the left inferior frontal gyrus.

Since the 1990s new research has shown that Broca's area contributes not just to speech but to music, mathematics and the understanding of complex manual actions. This recognition has reinvigorated the long-standing idea that toolmaking, along with the human propensity to communicate through gestures, may have served as pivotal evolutionary precursors to language. This idea has been most fully developed by Michael A. Arbib of the University of Southern California, for example, in his 2012 book *How the Brain Got Language*.

The results of our own imaging studies on stone toolmaking led us recently to propose that neural circuits, including the inferior frontal gyrus, underwent changes to adapt to the demands of Paleolithic toolmaking and then were co-opted to support primitive forms of communication using gestures and, perhaps, vocalizations. This protolinguistic communication would then have been subjected to selection, ultimately producing the specific adaptations that support modern human language. Our ongoing experiments, aside from building a massive mound of broken flint, will allow us to put this hypothesis to the test. SA

Dietrich Stout is a professor of anthropology at Emory University. His research focus on Paleolithic stone toolmaking integrates experimental methods from diverse disciplines, ranging from archaeology to brain imaging.

MORE TO EXPLORE

The Sapient Mind: Archaeology Meets Neuroscience. Edited by Colin Renfrew, Chris Frith and Lambros Malafouris. Oxford University Press, 2009.

Experimental Evidence for the Co-evolution of Hominin Tool-Making Teaching and Language. T.J.H. Morgan et al. in *Nature Communications*, Vol. 6, Article 6029; January 13, 2015.

Cognitive Demands of Lower Paleolithic Toolmaking. Dietrich Stout et al. in *PLOS ONE*, Vol. 10, No. 4, Article e0121804; April 15, 2015.

Dietrich Stout's publications: **https://scholarblogs.emory.edu/stoutlab/publications**

scientificamerican.com/magazine/sa

CAVE TODAY known simply as PP13B, near Mossel Bay, South Africa, sheltered humans between 164,000 and 35,000 years ago, at a time when *Homo sapiens* was in danger of dying out. These people may have been the ancestors of us all.

When the Sea Saved Humanity

Shortly after *Homo sapiens* arose, harsh climate conditions nearly extinguished our species. The small population that gave rise to all humans alive today may have survived by exploiting a unique combination of resources along the southern coast of Africa

By Curtis W. Marean

WITH THE GLOBAL POPULATION OF HUMANS WELL BEYOND SEVEN billion, it is difficult to imagine that *Homo sapiens* was once an endangered species. Yet studies of the DNA of modern-day people indicate that, once upon a time, our ancestors did in fact undergo a dramatic population decline. Although scientists lack a precise timeline for the origin and near extinction of our species, we can surmise from the fossil record that our forebears arose throughout Africa shortly before 195,000 years ago. Back then the climate was mild and food was plentiful; life was good. But around 195,000 years ago, conditions began to deteriorate. The planet entered a long glacial stage known as Marine Isotope Stage 6 (MIS6) that lasted until roughly 123,000 years ago.

IN BRIEF

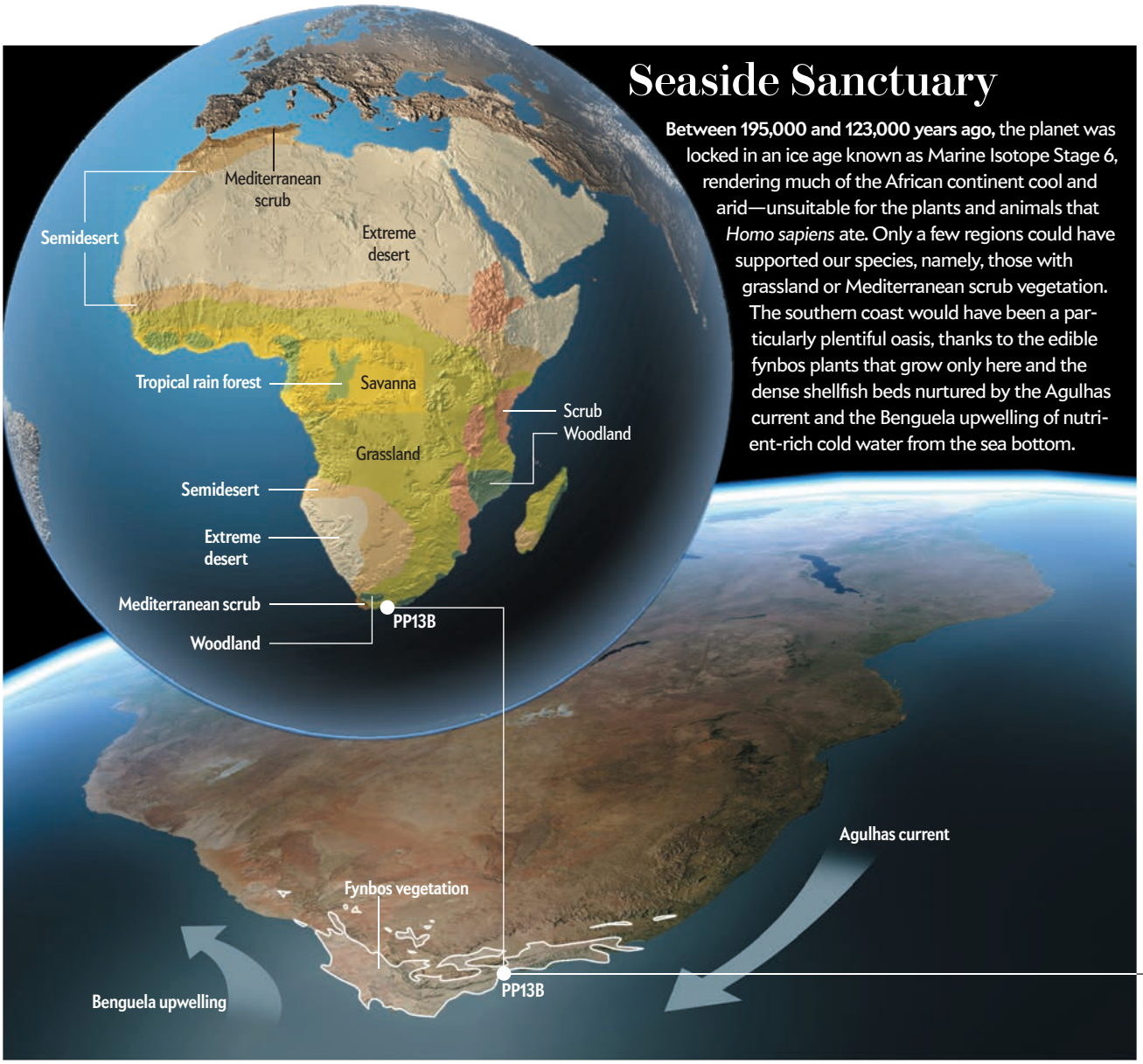
Sometime between 195,000 and 123,000 years ago, African *Homo sapiens* populations plummeted, thanks to cold, dry climate conditions that left much of the land uninhabitable. Everyone alive today is descended from people from a single region who survived this catastrophe.

The southern coast of Africa would have been one of the few spots where humans could survive during this climate crisis because it harbored an abundance of shellfish, mammals and edible plants.

Excavations of a series of sites in this region have recovered items left behind from this possible progenitor population.

The discoveries confirm the idea that advanced cognitive abilities evolved earlier than previously thought—and may have played a role in the survival of the species.

PER-ANDERS PETTERSON


Seaside Sanctuary
Between 195,000 and 123,000 years ago, the planet was locked in an ice age known as Marine Isotope Stage 6, rendering much of the African continent cool and arid—unsuitable for the plants and animals that *Homo sapiens* ate. Only a few regions could have supported our species, namely, those with grassland or Mediterranean scrub vegetation. The southern coast would have been a particularly plentiful oasis, thanks to the edible fynbos plants that grow only here and the dense shellfish beds nurtured by the Agulhas current and the Benguela upwelling of nutrient-rich cold water from the sea bottom.
Mediterranean scrub
Semidesert
Extreme desert
Tropical rain forest
Savanna
Scrub
Woodland
Grassland
Semidesert
Extreme desert
Mediterranean scrub
Woodland
PP13B
Agulhas current
Fynbos vegetation
Benguela upwelling
PP13B

A detailed record of Africa's environmental conditions during glacial stage 6 does not exist, but based on more recent, better-known glacial stages, climatologists surmise that it was almost certainly cool and arid and that its deserts were probably significantly expanded relative to their modern extents. Much of the landmass would have been uninhabitable. While the planet was in the grip of this icy regime, the number of people plummeted perilously—from more than 10,000 breeding individuals to just hundreds. Estimates of exactly when this bottleneck occurred and how small the population became vary among genetic studies, but all of them indicate that everyone alive today is descended from a small population that lived in one region of Africa sometime during this global cooling phase.

I began my career as an archaeologist working in East Africa and studying the origin of modern humans. But my interests began to shift when I learned of the population bottleneck that geneticists had started talking about in the early 1990s. Humans today exhibit very low genetic diversity relative to many other species with much smaller population sizes and geographic ranges—a phenomenon best explained by the occurrence of a population crash in early *H. sapiens*. Where, I wondered, did our ancestors manage to survive during the climate catastrophe? Only a handful of regions could have had the natural resources to support hunter-gatherers. Paleoanthropologists argue vociferously over which of these areas was the ideal spot. The southern coast of Africa, rich in shellfish and edible plants year-round, seemed to me as if it would have been a particularly good refuge in tough times. So, in 1991, I decided I would go there and look for sites with remains dating to glacial stage 6.

My search within that coastal area was not random. I had to find a shelter close enough to the ancient coastline to provide easy access to shellfish and elevated enough that its archaeological deposits would not have been washed away between 130,000 and 125,000 years ago, a period of transition when the climate warmed and sea levels surged. In 1999 my South African colleague Peter Nilssen and I decided to investigate some caves he

Don Foley (map), Lucy Reading-Ikkanda (globe)

PER-ANDERS PETTERSON

High and Dry

Finding archaeological sites dating to glacial stage 6 required searching for shelters that were close enough to the sea to allow relatively easy access to shellfish yet elevated enough that their ancient remains would not have washed away when the sea level rose 123,000 years ago. PP13B and other caves carved into the sheer cliff face of a promontory called Pinnacle Point meet those requirements and have yielded a plethora of remains dating to this critical juncture in human prehistory.

had spotted at a place called Pinnacle Point, a promontory near the town of Mossel Bay that juts into the Indian Ocean. Scrambling down the sheer cliff face, we came across a cave that looked particularly promising—one known simply as PP13B. Erosion of the sedimentary deposits located near the mouth of the cave had exposed clear layers of archaeological remains, including hearths and stone tools. Even better, a sand dune and a layer of stalagmite capped these remnants of human activity, suggesting that they were quite old. By all appearances, we had hit the jackpot. The following year, after a local ostrich farmer built us a 180-step wood staircase to allow safer access to the site, we began to dig.

Since then, my team's excavations at PP13B and other nearby sites have recovered a remarkable record of the activities undertaken by the people who inhabited this area between approximately 164,000 and 35,000 years ago, hence during the bottleneck and after the population began to recover. The deposits in these caves, combined with analyses of the ancient environment there, have enabled us to piece together a plausible account of how the prehistoric residents of Pinnacle Point eked out a living during a grim climate crisis. The remains also debunk the abiding notion that cognitive modernity evolved long after anatomical modernity: evidence of behavioral sophistication abounds in even the oldest archaeological levels at PP13B. This advanced intellect no doubt contributed significantly to the survival of the species, enabling our forebears to take advantage of the resources available on the coast.

While elsewhere on the continent populations of *H. sapiens* died out as cold and drought claimed the animals and plants they hunted and gathered, the lucky denizens of Pinnacle Point were feasting on the seafood and carbohydrate-rich plants that proliferated there despite the hostile climate. As glacial stage 6 cycled through its relatively warmer and colder phases, the seas rose and fell, and the ancient coastline advanced and retreated. But so long as people tracked the shore, they had access to an enviable bounty.

A COASTAL CORNUCOPIA

FROM A SURVIVAL STANDPOINT, what makes the southern edge of Africa attractive is its unique combination of plants and animals. There a thin strip of land containing the highest diversity of flora for its size in the world hugs the shoreline. Known as the Cape Floral Region, this 90,000-square-kilometer strip contains an astonishing 9,000 plant species, some 64 percent of which live only there. Indeed, the famous Table Mountain that rises above Cape Town in the heart of the Cape Floral Region has more species of plants than does the entire U.K. Of the vegetation groups that occur in this realm, the two most extensive are the fynbos and the renosterveld, which consist largely of shrubs. To a human forager equipped with a digging stick, they offer a valuable commodity: the plants in these groups produce the world's greatest diversity of geophytes—underground energy-storage organs such as tubers, bulbs and corms.

Geophytes are an important food source for modern-day hunter-gatherers, for several reasons. They contain high amounts of carbohydrate; they attain their peak carbohydrate content reliably at certain times of year; and, unlike aboveground fruits, nuts and seeds, they have few predators. The bulbs and corms that dominate the Cape Floral Region are additionally appealing because in contrast to the many geophytes that are highly fibrous, they are low in fiber relative to the amount of energy-rich carbohydrate they contain, making them more easily digested by children. (Cooking further enhances their digestibility.) And because geophytes are adapted to dry conditions, they would have been readily available during arid glacial phases. Recent studies in South Africa show that many of these species are easy to procure and rich in calories.

The southern coast also has an excellent source of protein to offer. Just offshore, the collision of nutrient-rich cold water from

1

2

3

Gone Shellfishing

Shellfish, which are rich in protein, are thought to have aided survival of the Pinnacle Point population because they abound year-round in the rocky intertidal zone along the southern coast of Africa (*1*). Brown mussels (*2*) have turned up in even the earliest levels of PP13B, dating to 164,000 years ago, revealing that humans began exploiting marine resources earlier than previously thought. In addition to mussels, the occupants of the Pinnacle Point sites collected various kinds of limpets as well as sea snails called alikreukel for food and gathered empty shells of helmet snails for their aesthetic appeal (*3*).

PER-ANDERS PETTERSON

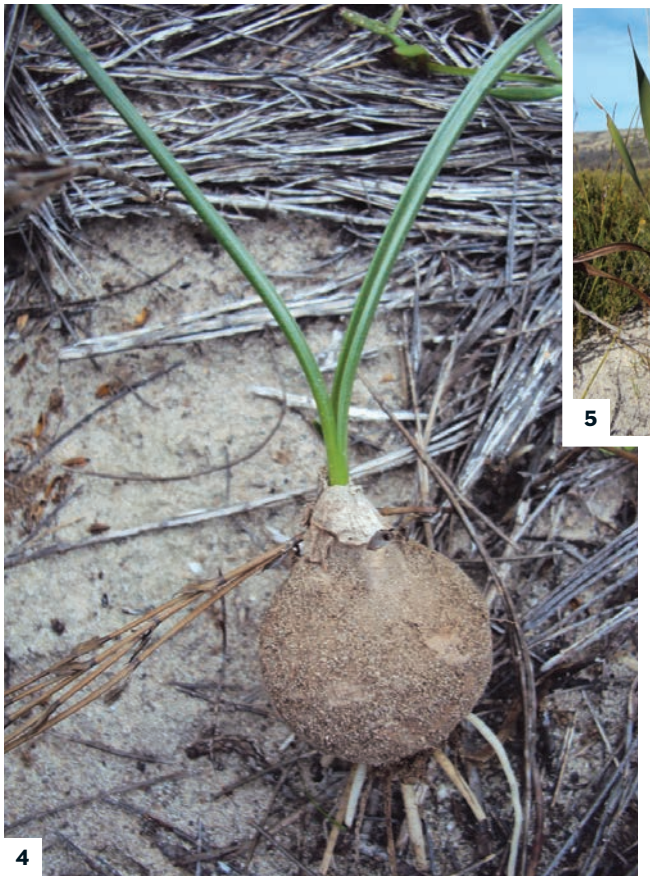
the Benguela upwelling and the warm Agulhas current creates a mix of cold and warm eddies along the southern coast. This varied ocean environment nurtures diverse and dense beds of shellfish in the rocky intertidal zones and sandy beaches. Shellfish are a very high quality source of protein and omega-3 fatty acids. And as with geophytes, glacial cooling does not depress their numbers. Rather, lower ocean temperatures result in a greater abundance of shellfish. Recent research by our team has shown that a potential third food resource was present during these glacial phases. When sea levels dropped, a plain was exposed in front of the caves, and migratory antelope moved east and west across it. The region, in short, provided an unprecedented concentration of food during glacial periods.

SURVIVAL SKILLS

EVEN WITHOUT ANTELOPE, the southern coast, with its combination of calorically dense, nutrient-rich protein from the shellfish and low-fiber, energy-laden carbs from the geophytes, would have provided an ideal diet for early modern humans during glacial stage 6. Furthermore, women could obtain both these resources on their own, freeing them from relying on men to provision them and their children with high-quality food. We have yet to unearth proof that the occupants of PP13B were eating geophytes—sites this old rarely preserve organic remains—although younger sites in the area contain extensive evidence of geophyte consumption. But we have found clear evidence that they were dining on shellfish. Studies of the shells found at the site conducted by Antonieta Jerardino, then at the University of Barcelona, show that people were gathering brown mussels and local sea snails called alikreukel from the seashore. They also ate marine mammals such as seals and whales on occasion.

Previously the oldest known examples of humans systematically using marine resources dated to less than 120,000 years ago. But dating analyses performed by Miryam Bar-Matthews of the Geological Survey of Israel and Zenobia Jacobs of the University of Wollongong in Australia have revealed that the PP13B people lived off the sea far earlier than that: as we reported in 2007 in the journal *Nature,* marine foraging there dates back to a stunning 164,000 years ago. By 110,000 years ago the menu had expanded to include species such as limpets and sand mussels.

This kind of foraging is harder than it might seem. The mussels, limpets and sea snails live on the rocks in the treacherous intertidal zone, where an incoming swell could easily knock over a



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Digging for Dinner

Geophytes, the underground energy-storage organs of certain kinds of plants (*4*), swell with edible carbohydrates at certain times of the year. The distinctive vegetation that hugs the southern coast of Africa, particularly the fynbos plants (*5*), produces especially nutritious and easily digested geophytes, which presumably served as a staple for the early modern humans who lived in this region during glacial stage 6.

hapless collector. Along the southern coast, safe harvesting with sufficiently high returns is only possible during low spring tides, when the sun and moon align, exerting their maximum gravitational force on the ebb and flow of the water. Because the tides are linked to the phases of the moon, advancing by 50 minutes a day, I surmise that the people who lived at PP13B—which 164,000 years ago was located much farther inland, two to five kilometers from the water, because of lower sea levels—scheduled their trips to the shore using a lunar calendar of sorts, just as modern coastal people have done for ages.

Harvesting shellfish is not the only advanced behavior in evidence at Pinnacle Point as early as 164,000 years ago. Among the stone tools are significant numbers of "bladelets"—tiny flakes twice as long as they are wide—that are too small to wield by hand. Instead they must have been attached to shafts of wood and used as projectile weapons. Composite toolmaking is indicative of considerable technological know-how, and the bladelets at PP13B are among the oldest examples of it. But we soon learned that these tiny implements were even more complex than we thought.

Most of the stone tools found at coastal South African archaeological sites are made from a type of stone called quartzite. This coarse-grained rock is great for making large flakes, but it is difficult to shape into small, refined tools. To manufacture the bladelets, people used fine-grained rock called silcrete. There was something odd about the archaeological silcrete, though, as observed by Kyle S. Brown of the Institute of Human Origins at Arizona State University, an expert stone tool flaker on my team. After years of collecting silcrete from all over the coast, Brown determined that in its raw form the rock never has the lustrous red and gray coloring seen in the silcrete implements at Pinnacle Point and elsewhere. Furthermore, the raw silcrete is virtually impossible to shape into bladelets. Where, we wondered, did the toolmakers find their superior silcrete?

A possible answer to this question came from another site we are excavating, Pinnacle Point Cave 5-6 (PP5-6), where one day in 2008 we found a large piece of silcrete embedded in ash. It had the same color and luster seen in the silcrete found at other archaeological deposits in the region. Given the association of the stone with the ash, we asked ourselves whether the ancient toolmakers might have exposed the silcrete to fire to make it easier to work with—a strategy that has been documented in ethnographic accounts of native North Americans and Australians. To find out, Brown carefully "cooked" some raw silcrete and then attempted to knap it. It flaked wonderfully, and the flaked surfaces shone with the same luster seen in the artifacts from our sites. We thus concluded that the Stone Age silcrete was also heat-treated.

We faced an uphill battle to convince our colleagues of this remarkable claim, however. It was archaeology gospel that the Solutrean people in France invented heat treatment about 20,000 years ago, using it to make their beautiful tools. To bolster our case, we used three independent techniques. Chantal Tribolo of the University of Bordeaux Montaigne performed what is called thermoluminescence analysis to determine whether the silcrete tools from Pinnacle Point were intentionally heated. Then Andy Herries, at the time at the University of New South Wales in Australia, employed magnetic susceptibility, which looks for changes in the ability of rock to be magnetized—another indicator of heat exposure among iron-rich rocks. Finally, Brown used a gloss meter to measure the luster that develops after heating and flaking and compared it with the luster on the tools he made. Our results, published in 2009 in *Science,* showed that intentional heat treatment was a dominant technology at Pinnacle Point by 72,000 years ago and that people there employed it intermittently as far back as 164,000 years ago. In 2012 we showed that Pinnacle Point residents employed an entirely new technique of stone tool manufacture, called microlithic technology, far earlier than anywhere else in the world. This technology allows one to make very small, light stone weapons and represents a breakthrough in the lethality of armaments.

The process of treating by heat testifies to two uniquely mod-

COURTESY OF J. C. DE VYNCK *Center for Coastal Paleosciences, Nelson Mandela Metropolitan University*

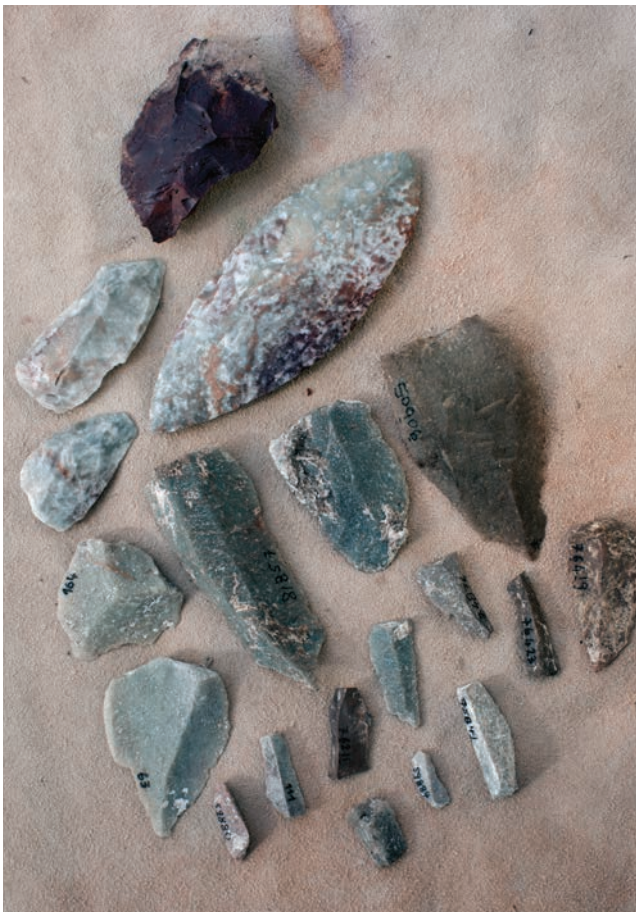
ern human cognitive abilities. First, people recognized that they could substantially alter a raw material to make it useful—in this case, engineering the properties of stone by heating it, thereby turning a poor-quality rock into high-quality raw material. Second, they could invent and execute a long chain of processes. The making of silcrete blades requires a complex series of carefully designed steps: building a sand pit to insulate the silcrete, bringing the heat slowly up to 350 degrees Celsius, holding the temperature steady and then dropping it down slowly. Creating and carrying out the sequence and passing technologies down from generation to generation probably required language. Once established, these abilities no doubt helped our ancestors outcompete the archaic human species they encountered once they dispersed from Africa. In particular, the complex pyrotechnology detected at Pinnacle Point would have given early modern humans a distinct advantage as they entered the cold lands of the Neandertals, who seem to have lacked this technique.

SMART FROM THE START

IN ADDITION to being technologically savvy, the prehistoric denizens of Pinnacle Point had an artistic side. In the oldest layers of the PP13B sequence, my team has unearthed dozens of pieces of red ochre (iron oxide) that were variously carved and ground to create a fine powder that was probably mixed with a binder such as animal fat to make paint that could be applied to the body or other surfaces. Such decorations typically encode information about social identity or other important aspects of culture—that is, they are symbolic. Many of my colleagues and I think that this ochre constitutes the earliest unequivocal example of symbolic behavior on record and pushes the origin of such practices back by tens of thousands of years. Evidence of symbolic activities also appears later in the sequence. Deposits dating to around 110,000 years ago include both red ochre and seashells that were clearly collected for their aesthetic appeal because by the time they washed ashore from their deepwater home, any flesh would have been long gone. I think these decorative seashells, along with the evidence for marine foraging, signal that people had, for the first time, begun to embed in their worldview and rituals a clear commitment to the sea.

The precocious expressions of both symbolism and sophisticated technology at Pinnacle Point have major implications for understanding the origin of our species. Fossils from Ethiopia show that anatomically modern humans had evolved by at least 195,000 years ago. The emergence of the modern mind, however, is more difficult to establish. Paleoanthropologists use various proxies in the archaeological record to try to identify the presence and scope of cognitive modernity. Artifacts made using technologies that require outside-the-box connections of seemingly unrelated phenomena and long chains of production—like heat treatment of rock for tool manufacture—are one proxy. Evidence of art or other symbolic activities is another, as is the tracking of time through proxies such as lunar phases. For years the earliest examples of these behaviors were all found in Europe and dated to after 40,000 years ago. Based on that record, researchers concluded that there was a long lag between the origin of our species and the emergence of our peerless creativity.

But over the past 15 or so years archaeologists working at a number of sites in South Africa have found examples of sophisticated behaviors that predate by a long shot their counterparts in Europe. For instance, archaeologist Ian Watts, who works in South Africa, has described hundreds to thousands of pieces of worked and unworked ochre at sites dating as far back as 120,000 years ago. Interestingly, this ochre, as well as the pieces at Pinnacle Point, tends to be red despite the fact that local sources of the mineral exhibit a range of hues, suggesting that humans were preferentially curating the red pieces—perhaps associating the color with menstruation and fertility. Jocelyn A. Bernatchez, who earned her Ph.D. at Arizona State, thinks that many of these ochre pieces may have been yellow originally and then heat-treated to turn them red. And at Blombos Cave, located about 100 kilometers west of Pinnacle Point, Christopher S. Henshilwood of the Universities of Bergen in Norway and Witwatersrand, Johannesburg, in South Africa has discovered pieces of ochre with systematic engravings, beads made of snail shells and refined bone tools, all of which date to around 71,000 years ago. These sites, along with those at Pinnacle Point, belie the claim that modern cognition evolved late in our lineage and suggest instead that our species had this faculty at its inception.



Cutting-Edge Technology

Stone tools found in PP13B include sophisticated implements such as microblades (*bottom two rows*), which would have been attached to a wood shaft to form projectile weapons. The toolmakers also appear to have heat-treated the stone to make it easier to shape—a technique that was believed to have originated much later and in France.

PER-ANDERS PETTERSON

PER-ANDERS PETTERSON

Probing the Past

Continued excavation of PP13B (*shown here*) and other caves along the southern coast of Africa should reveal more about the progenitor population of humans who survived the population bottleneck and went on to colonize the globe.

I suspect that a driving force in the evolution of this complex cognition was strong long-term selection acting to enhance our ancestors' ability to mentally map the location and seasonal variation of many species of plants in arid environments and to convey this accumulated knowledge to offspring and other group members. This capacity laid the foundation for many other advances, such as the ability to grasp the link between the phases of the moon and the tides and to learn to schedule their shellfish-hunting trips to the shore accordingly. Together the readily available shellfish and other abundant foods provided a high-quality diet that allowed people to become less nomadic, increased their birth rates and reduced their child mortality. The larger group sizes that resulted from these changes would have promoted symbolic behavior and technological complexity as people endeavored to express their social identity and build on one another's technologies, explaining why we see such sophisticated practices at PP13B.

FOLLOW THE SEA

PP13B PRESERVES a long record of changing occupations that, in combination with the detailed records of local climate and environmental change my team has obtained, is revealing how our ancestors used the cave and the coast over millennia. Modeling the paleocoastline over time, Erich C. Fisher of the University of Florida has shown that the conditions changed quickly and dramatically, thanks to a long, wide, gently sloping continental shelf off the coast of South Africa called the Agulhas bank. During glacial periods, when sea levels fell, significant amounts of this shelf would have been exposed, putting considerable distance—up to 95 kilometers—between Pinnacle Point and the ocean. When the climate warmed and sea levels rose, the water advanced over the Agulhas bank again, and the caves were seaside once more.

Judging from rainfall and vegetation patterns evident in records from stalagmites spanning the time between 350,000 and 50,000 years ago, we see that the fynbos probably followed the retreating coast out onto the now submerged continental shelf and back again, keeping the geophytes and shellfish in close proximity. As for the people, during these periods of low population density they were free to target the best part of the landscape, and that was the intersection of the geophytes and shellfish—so I suspect they followed the sea. The tracking of resources would explain why PP13B appears to have been occupied intermittently.

Our excavations at PP13B have intercepted the people who may very well be the ancestors of everyone on the planet as they shadowed the shifting shoreline. Yet if I am correct about these people and their connection to the coast, the richest record of the progenitor population lies underwater on the Agulhas bank. There it will remain for the near future, guarded by great white sharks and dangerous currents. We can still test the hypothesis that humans followed the sea by examining sites on the current coast such as PP13B and PP5-6. But we can also study locations where the continental shelf drops steeply and the coast was always near—investigations that Fisher and I are currently running on the eastern coast of Africa in Pondoland.

The genetic, fossil and archaeological records are reasonably concordant in suggesting that the first substantial and prolonged wave of modern human migration out of Africa occurred around 50,000 years ago. But questions about the events leading up to that exodus remain. We still do not know, for example, whether at the end of glacial stage 6 there was just one population of *H. sapiens* left in Africa or whether there were several, with just one ultimately giving rise to everyone alive today. Such unknowns are providing my team and others with a very clear and exciting research direction for the foreseeable future: our fieldwork needs to target the other potential progenitor zones in Africa during that glacial period and expand our knowledge of the climate conditions just before that stage. We need to flesh out the story of these people who eventually pushed out of their refuge, filled up the African continent and went on to conquer the world. SA

Curtis W. Marean is honorary professor at the Center for Coastal Palaeoscience at Nelson Mandela Metropolitan University in South Africa. He studies the origins of modern humans, the prehistory of Africa, paleoclimates and paleoenvironments, and animal bones from archaeological sites. Marean is particularly interested in human occupation of coastal ecosystems. He is the principal investigator for the South African Coast Paleoclimate, Paleoenvironment, Paleoecology, Paleoanthropology (SACP4) project, funded by the National Science Foundation.

MORE TO EXPLORE

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Human Hybrids

DNA analyses find that early *Homo sapiens* mated with other human species and hint that such interbreeding played a key role in the triumph of our kind

By Michael F. Hammer

IT IS HARD TO IMAGINE TODAY, BUT FOR MOST OF HUMANKIND'S evolutionary history, multiple humanlike species shared the earth. As recently as 40,000 years ago, *Homo sapiens* lived alongside several kindred forms, including the Neandertals and tiny *Homo floresiensis*. For decades scientists have debated exactly how *H. sapiens* originated and came to be the last human species standing. Thanks in large part to genetic studies in the 1980s, one theory emerged as the clear front-runner. In this view, anatomically modern humans arose in Africa and spread out across the rest of the Old World, completely replacing the existing archaic groups. Exactly how this novel form became the last human species on the planet is mysterious. Perhaps the invaders killed off the natives they encountered, or outcompeted the strangers on their own turf or simply reproduced at a higher rate. However it happened, the newcomers seemed to have eliminated their competitors without interbreeding with them.

IN BRIEF

A long-reigning theory of the origin of *Homo sapiens* holds that our species arose in a single locale—sub-Saharan Africa—and replaced archaic human species, such as the Neandertals, without interbreeding with them.

But recent studies of modern and ancient DNA indicate that these modern humans from Africa did mate with archaic humans and hint that this interbreeding helped *H. sapiens* thrive as it colonized new lands.

Illustration by Brian Stauffer

This Recent African Replacement model, as it is known, has essentially served as the modern human origins paradigm for the past 30 or so years. Yet mounting evidence indicates that it is wrong. Recent advances in DNA-sequencing technology have enabled researchers to dramatically scale up data collection from living people as well as from extinct species. Analyses of these data with increasingly sophisticated computational tools indicate that the story of our family history is not as simple as most experts thought. It turns out that people today carry DNA inherited from Neandertals and other archaic humans, revealing that early *H. sapiens* mated with these other species and produced fertile offspring who were able to hand this genetic legacy down through thousands of generations. In addition to upsetting the conventional wisdom about our origins, the discoveries are driving new inquiries into how extensive the interbreeding was, which geographical areas it occurred in and whether modern humans show signs of benefiting from any of the genetic contributions from our prehistoric cousins.

MYSTERIOUS ORIGINS

TO FULLY APPRECIATE the effect of these recent genetic findings on scientists' understanding of human evolution, we must look back to the 1980s, when the debate over the rise of *H. sapiens* was heating up. Examining the fossil data, paleoanthropologists agreed that an earlier member of our genus, *Homo erectus*, arose in Africa some two million years ago and began spreading out of that continent and into other regions of the Old World shortly thereafter. Yet they disagreed over how the ancestors of *H. sapiens* transitioned from that archaic form to our modern one, with its rounded braincase and delicately built skeleton—features that appear in the fossil record at around 195,000 years ago.

Proponents of the so-called Multiregional Evolution model, developed by Milford H. Wolpoff of the University of Michigan and his colleagues, argued that the transformation occurred gradually among archaic populations wherever they lived throughout Africa, Eurasia and Oceania because of a combination of migration and mating that allowed beneficial modern traits to spread among all these populations. In this scenario, although all modern humans shared particular physical features by the end of this transition, some regionally distinctive features inherited from archaic ancestors persisted, perhaps because these traits helped populations to adapt to their local environments. A variant of the Multiregional Evolution model put forward by Fred Smith, now at Illinois State University, called the Assimilation model, acknowledges a greater contribution of modern traits by populations from Africa.

In contrast, champions of the Replacement model (also known as the Out of Africa model, among other names), including Christopher Stringer of the Natural History Museum in London, contended that anatomically modern humans arose as a distinct species in a single place—sub-Saharan Africa—and went on to completely replace all archaic humans everywhere without interbreeding with them. A looser version of this theory—the Hybridization model proposed by Günter Bräuer of the University of Hamburg in Germany—allows for the occasional production of hybrids between these modern humans and the archaic groups they met up with as they pushed into new lands.

With only the fossil evidence to go on, the debate seemed locked in a stalemate. Genetics changed that situation. With the advent of DNA technology, scientists developed methods for piecing together the past by analyzing genetic variation in contemporary human populations and using it to reconstruct evolutionary trees for individual genes. By studying a gene tree, researchers could infer when and where the last common ancestor of all the variants of a given gene existed, thus yielding insights into the population of origin for the ancestral sequence.

In a landmark study published in 1987, Allan C. Wilson of the University of California, Berkeley, and his colleagues reported that the evolutionary tree for the DNA found in mitochondria—the energy-producing components of cells—traced back to a female ancestor who lived in an African population around 200,000 years ago. (Mitochondrial DNA, or mtDNA, is passed down from mother to child and treated as a single gene in ancestry studies.) These findings fit the expectations of the Replacement model, as did subsequent studies of small sections of nuclear DNA, including the paternally inherited Y chromosome.

Further genetic support for the Replacement model came a decade later, when Svante Pääbo, now at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, and his colleagues succeeded in extracting and analyzing a fragment of mtDNA from Neandertal bones. The study found that the Neandertal mtDNA sequences were distinct from those of contemporary humans and that there was no sign of interbreeding between them—a result that subsequent studies of mtDNA from additional Neandertal specimens confirmed.

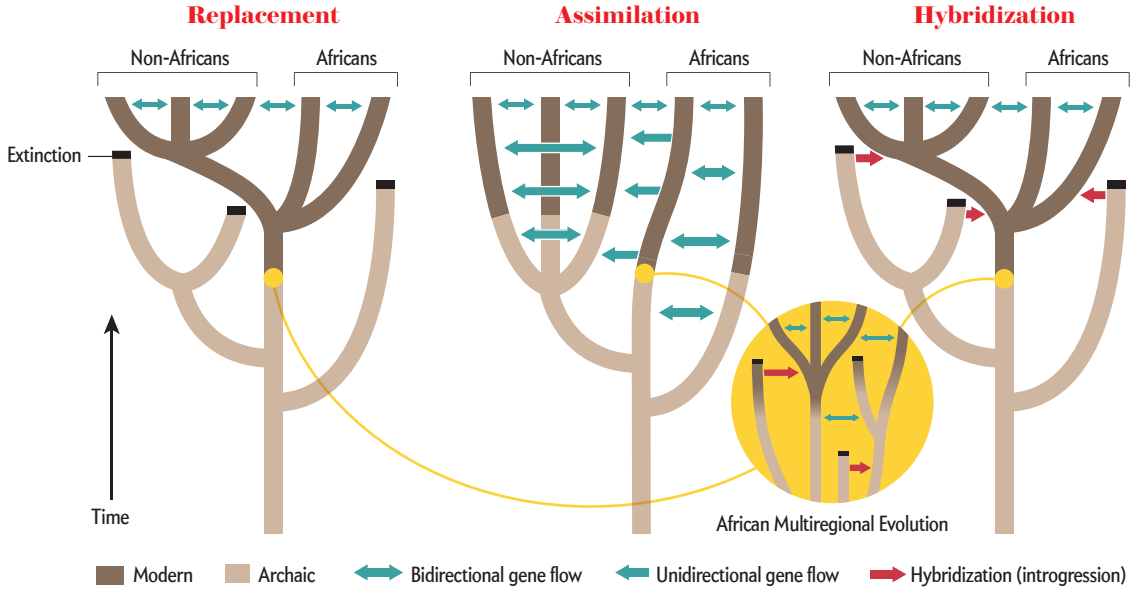
To many researchers, these ancient mtDNA findings put the nail in the coffin of the Multiregional Evolution and Assimilation models. Others, however, maintained that their reasoning suffered from a fundamental problem. The absence of a signal for interbreeding in any single independent region of the genome, such as in mtDNA, does not necessarily mean that other regions of the genome also lack signs of interbreeding. Further, any particular region of the genome that is tested could lack signs of interbreeding even if interbreeding did occur because DNA from other species (introgressed DNA) that provided no survival advantage to *H. sapiens* would tend to disappear from the gene pool over time by chance.

The best way to approach the question of whether *H. sapiens* interbred with archaic species, such as the Neandertals, is thus to compare many regions of their genomes or, ideally, their entire genomes. Yet even before such data became available for archaic humans, some early genetic studies of modern human DNA bucked the majority trend and found data contrary to the Replacement model. One clear example came from a 2005 study led by Daniel Garrigan, then a postdoctoral researcher in my laboratory. Garrigan looked at DNA sequences from a nonfunctional region of the X chromosome known as RRM2P4. Analyses of its reconstructed tree pointed to an origin for the sequence, not in Africa but in East Asia around 1.5 million years ago, implying that the DNA came from an archaic Asian species that intermixed with the *H. sapiens* originally from Africa. Similarly, that same year our lab discovered variation in another nonfunctional region of the X chromosome, Xp21.1, with a gene tree showing two divergent branches that had probably been evolving in complete isolation from each other for around a million years. One of these branches was presumably introduced into anatomically modern populations by an archaic African species. The RRM2P4 and Xp21.1 evidence thus hinted that anatomically modern hu-

COMPETING THEORIES

Sourcing *Homo sapiens*

Scientists have long debated how anatomically modern humans (*dark brown lines*) evolved from their archaic predecessors (*light brown lines*). In the theories depicted here, modern humans originated in Africa. According to the Replacement model, they then replaced archaic human species throughout the Old World without interbreeding with them. The Assimilation model, in contrast, holds that beneficial modern features from Africa spread among these archaic groups by a combination of steady migration and mating among individuals known as gene flow (*green arrows*). The Hybridization model, for its part, posits that populations of modern humans interbred, or hybridized (*red arrows*), on rarer occasions with smaller groups of archaic species as they encountered them. The African Multiregional Evolution model focuses exclusively on the archaic-to-modern transition period in Africa and argues for gene flow and hybridization between distinctive archaic groups there.



SOURCE: MICHAEL F. HAMMER

mans mated with archaic humans from Asia and Africa, respectively, rather than simply replacing them without interbreeding.

OUR ARCHAIC DNA

MORE RECENTLY, advances in sequencing technology have enabled scientists to quickly sequence entire nuclear genomes—including those of extinct humans, such as Neandertals. In 2010 Pääbo's group reported that it had reconstructed the better part of a Neandertal genome, based on DNA from several Neandertal fossils from Croatia. Contrary to the team's expectations, the work revealed that Neandertals made a small but significant contribution to the modern human gene pool: non-Africans today exhibit a 1 to 4 percent Neandertal contribution to their genomes on average. To explain this result, the researchers proposed that interbreeding between Neandertals and the ancestors of all non-Africans probably occurred during the limited period when these two groups overlapped in the Middle East, perhaps 80,000 to 50,000 years ago.

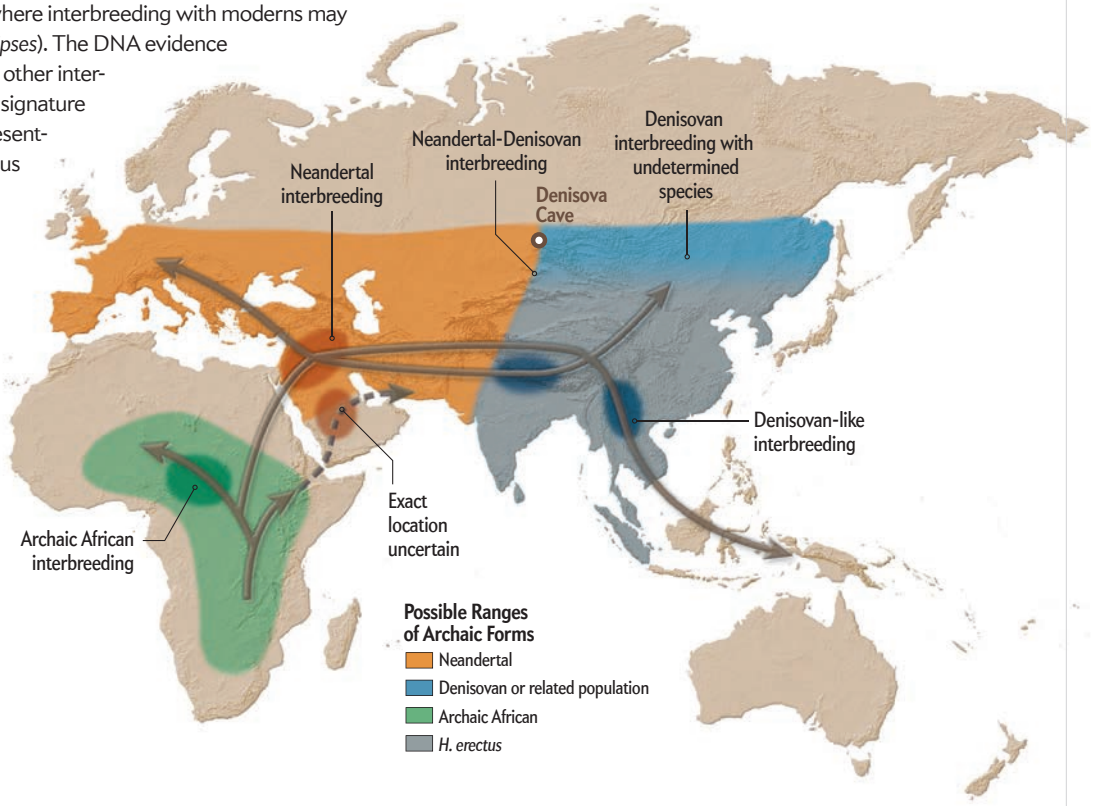
Hot on the heels of the Neandertal genome announcement, Pääbo's team revealed an even more startling discovery. The researchers had obtained an mtDNA sequence from a piece of an approximately 40,000-year-old finger bone found in Denisova Cave in the Altai Mountains in Siberia. Although researchers could not determine from the anatomy of the bone what species it represented, the genome sequence showed that this individual belonged to a population that was slightly more closely related to Neandertals than it or Neandertals were to our species. Further, after comparing the Denisovan sequence with its counterpart in modern populations, the team found a significant amount of DNA from a Denisovan-like population—a contribution of 1 to 6 percent—in Melanesians, Aboriginal Australians, Polynesians, and some related groups in the western Pacific but not in Africans or Eurasians.

To explain this increasingly complex pattern of DNA sharing, researchers proposed two interbreeding events between modern human and archaic populations: the first, with Neandertals, when anatomically modern humans initially migrated out of Africa; and the second, with Denisovan-like humans, when the descendants of these initial migrants made their way to Southeast Asia. The most recent evidence, however, supports several additional interbreeding occurrences—for example, between early modern non-Africans in the Near East that introduced genes into the ancestors of a subset of Neandertals and in other cases in which genes were exchanged between different archaic populations. The evidence also points to at least one additional event that boosted the Neandertal contribution to contemporary populations now living in East Asia. And the previously inferred gene flow from a Denisovan-like population into modern hu-

Graphic by Jen Christiansen

Evidence for Interbreeding

The fossil record indicates that *H. sapiens* originated in Africa by around 200,000 years ago. DNA studies suggest that these anatomically modern humans mated with archaic humans during migrations within Africa and out into the rest of the Old World (*gray arrows*). The map shows possible ranges of archaic species (including one identified through a finger bone from Denisova Cave in Siberia) and regions where interbreeding with moderns may have occurred (*five ellipses*). The DNA evidence implies that these and other interbreeding events left a signature on the genomes of present-day humans and various archaic forms. Some archaic species are known to have existed only because their DNA appears in fossils, in the fossils of other species or in our gene pool.



man populations in Melanesia is now believed to have left a more widespread DNA signature in present-day East Asian and Native America populations.

Although discussion of interbreeding in human evolution typically focuses on mating between anatomically modern humans and Neandertals in Europe or other archaic forms in Asia, the greatest opportunity for interspecies coupling would have been in Africa, where anatomically modern humans and various archaic forms coexisted for much longer than they did anywhere else. Unfortunately, the tropical environments of the African rain forest do not favor the preservation of DNA in ancient remains. Without an African ancient DNA sequence to reference, geneticists are currently limited to scouring the genomes of modern-day Africans for signs of archaic interbreeding.

To that end, PingHsun Hsieh in my lab aimed to test the hypothesis of interbreeding between archaic and modern humans in Africa without using ancient DNA from archaic human fossils. We analyzed whole-genome sequence data from two contemporary Central African Pygmy hunter-gatherer populations and identified more than 250 genetic loci with strong archaic DNA signals. Our inferences provided evidence for more than a single mixing event between unidentified African archaic forms and anatomically modern Africans, with at least one such event occurring within the past 30,000 years.

Another genetic hint of archaic interbreeding in Africa has come from a study of an unusual Y chromosome sequence obtained from an African-American man living in South Carolina whose DNA was submitted to a direct-to-consumer genetic testing company for analysis. His particular variant had never been seen before. Comparing his Y sequence against those of other humans, as well as chimpanzees, my team determined that his sequence represents a previously unknown Y chromosome lineage that increased the age of the common ancestor of contemporary Y chromosomes. We then searched a database of nearly 6,000 African Y chromosomes and identified 11 matches—all of which came from men who lived in a very small area of western Cameroon. Recently Fernando Mendez and his Stanford University collaborators reestimated the age of the time to the most recent common Y chromosome ancestor at 275,000 years, significantly older than the time of appearance of anatomically modern fossils in Africa. The presence of this very ancient lineage in contemporary people is a possible sign of interbreeding between *H. sapiens* and an unknown archaic species in western Central Africa.

SOURCE: "GENOMIC DATA REVEAL A COMPLEX MAKING OF HUMANS," BY ISABEL ALVES ET AL., IN *PLOS GENETICS*, VOL. 8, NO. 7; JULY 19, 2012

Map by XNR Productions

Recently the fossil record, too, has yielded support for the possibility of interbreeding within Africa. Just after the publication of our results in 2011, a group of paleontologists working at the Iwo Eleru site in Nigeria reanalyzed remains that exhibit cranial features intermediate between those of archaic and modern humans and determined that they date to just 13,000 years ago—long after anatomically modern *H. sapiens* had debuted. These results, along with similar findings from the Ishango site in the Democratic Republic of the Congo, suggest that the evolution of anatomical modernity in Africa may have been more complicated than any of the leading models for modern human origins have envisioned. Either archaic humans lived alongside modern ones in the recent past, or populations with both modern and archaic features interbred over millennia.

BENEFICIAL CONTRIBUTIONS?

DETAILED STUDIES OF DNA regions inherited from archaic ancestors will help tackle the question of whether interbreeding (and subsequently genetic variation) conferred an adaptive advantage to early *H. sapiens*. Indeed, there are now several examples involving archaic gene regions closely related to Neandertal and Denisovan genomes that are found at particularly high frequency in contemporary human populations. Approximately 10 percent of people from Eurasia and Oceania carry the Neandertal-like variant of *STAT2*, which is involved in the body's first line of defense against viral pathogens. Interestingly, it occurs at a roughly 10-fold higher frequency in Melanesia than in East Asia. Analysis suggests that this DNA segment rose to high frequency through positive natural selection (that is, because it aided reproductive success or survival) rather than merely by chance, implying that it benefited the anatomically modern populations of Melanesia. It is not surprising to find archaic contributions containing genes that function to increase immunity. It is easy to imagine that the acquisition of a gene variant that is adapted to fending off pathogens in non-African environments would immediately benefit human ancestors as they expanded from Africa into new habitats.

Perhaps the most dramatic example of shared gene variants involves the gene *EPAS1*, involved in the body's response to low oxygen levels. DNA sequence variants at this gene were initially shown to confer adaptation to high altitude in Tibetans; subsequently these variants were found to be inherited from a Denisovan-like ancestor. Other examples of adaptively introgressed genetic variants include genes involved in hair and skin biology and lipid metabolism. Interestingly, genetic variation inherited from Neandertals may raise the risk of human diseases, including those associated with psychiatric, neurological, immunological and dermatological conditions.

In light of the accumulating evidence for interbreeding between anatomically modern *H. sapiens* and archaic humans both inside Africa and beyond its confines, the Replacement model is no longer tenable. Modern and archaic species of *Homo* were able to produce viable hybrid offspring. Thus, archaic forms could go extinct while still leaving behind their genetic footprints in the modern human genome. That said, the genomes of people today seem to derive mostly from African ancestors—contributions from archaic Eurasians are smaller than either the Multiregional Evolution or Assimilation model predicts.

A number of researchers now favor Bräuer's Hybridization model, which holds that mating between *H. sapiens* and archaic species was limited to a few isolated instances. But given the current picture both inside and outside Africa, I favor models in which interbreeding was more common in the history of our species. Given the complexity of the African fossil record, which indicates that a variety of transitional human groups, with a mosaic of archaic and modern features, lived over an extensive geographic area from Morocco to South Africa between roughly 200,000 and 35,000 years ago, I lean toward a model that involves interspecies mating during the archaic-to-modern transition. Sometimes called African Multiregional Evolution, this scenario allows for the possibility that some of the traits that make us anatomically modern were inherited from transitional forms before they went extinct. To my mind, the African Multiregional Evolution model best explains genetic and fossil data to date.

THE ROOTS OF MODERN HUMANS TRACE BACK TO NOT JUST A SINGLE ANCESTRAL POPULATION IN AFRICA BUT TO POPULATIONS THROUGHOUT THE OLD WORLD.

Before scientists can assess this model for modern human origins fully, we will need to better understand which genes code for anatomically modern traits and decipher their evolutionary history. Further analysis of both archaic and modern genomes should aid researchers in pinpointing when and where mixing occurred—and whether the archaic genes that entered the modern human gene pool benefited the populations that acquired them. This information will help us evaluate the hypothesis that interbreeding with archaic populations that were well adapted to their local environments lent traits to *H. sapiens* that spurred its rise to global preeminence. The sharing of genes through occasional interspecies mating is one way that evolutionary novelties arise in many species of animals and plants, so it should not be surprising if the same process occurred in our own past.

Many loose ends remain. Yet one thing is clear: the roots of modern humans trace back to not just a single ancestral population in Africa but to populations throughout the Old World. Although archaic humans have often been seen as rivals of modern humans, scientists now must seriously consider the possibility that they were the secret of *H. sapiens*' success. SA

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MORE TO EXPLORE

A High-Coverage Genome Sequence from an Archaic Denisovan Individual. Matthias Meyer et al. in *Science*, Vol. 338, pages 222–226; October 12, 2012.

An African American Paternal Lineage Adds an Extremely Ancient Root to the Human Y Chromosome Phylogenetic Tree. Fernando L. Mendez et al. in *American Journal of Human Genetics*, Vol. 92, No. 3, pages 454–459; February 28, 2013.

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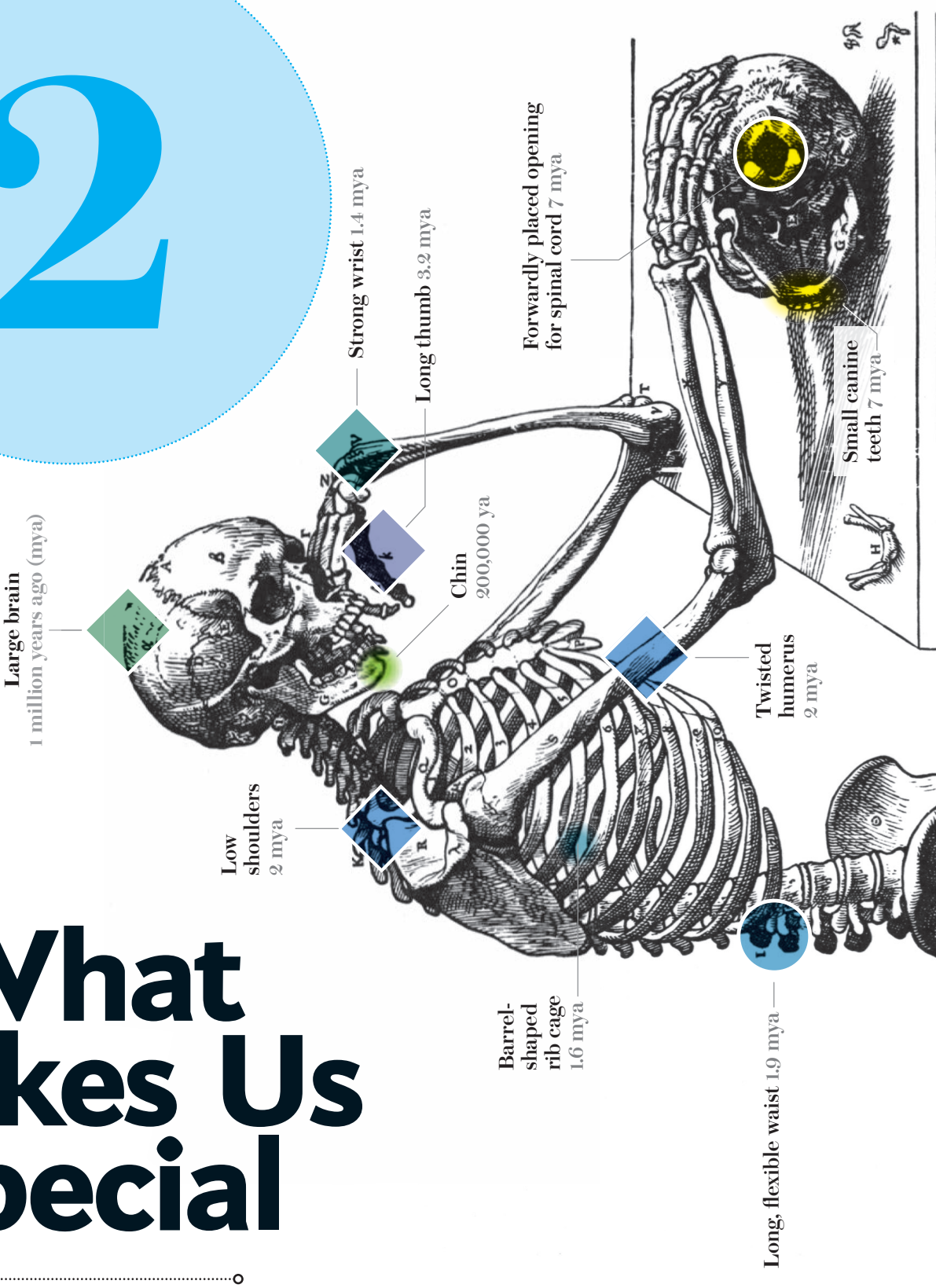
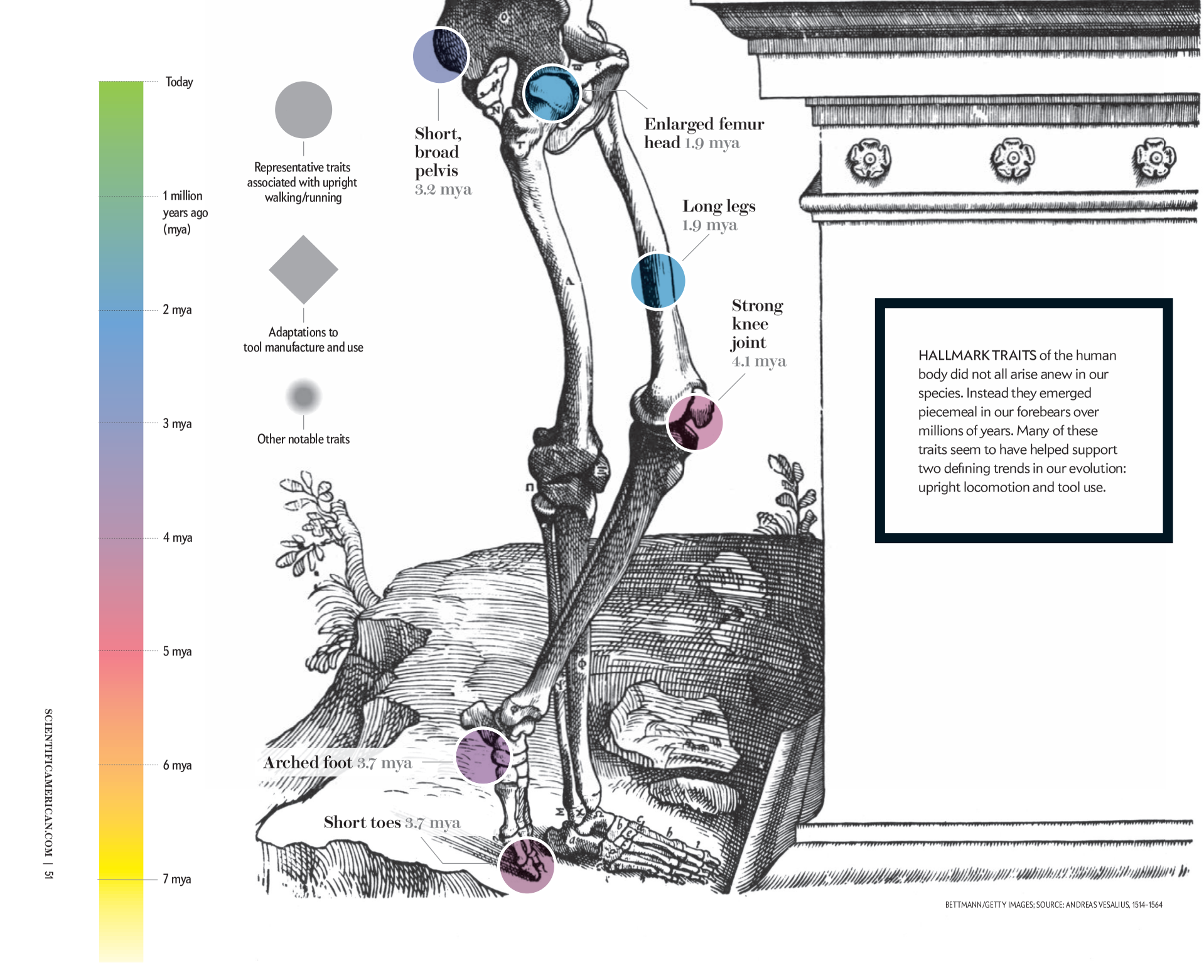
What Makes Us Special





HALLMARK TRAITS of the human body did not all arise anew in our species. Instead they emerged piecemeal in our forebears over millions of years. Many of these traits seem to have helped support two defining trends in our evolution: upright locomotion and tool use.

BETTMANN/GETTY IMAGES; SOURCE: ANDREAS VESALIUS, 1514–1564

The Naked Truth

Recent findings lay bare the origins of human hairlessness—and hint that naked skin was a key factor in the emergence of other human traits

By Nina G. Jablonski

AMONG PRIMATES, HUMANS ARE UNIQUE IN HAVING NEARLY NAKED SKIN. Every other member of our extended family has a dense covering of fur—from the short, black pelage of the howler monkey to the flowing copper coat of the orangutan—as do most other mammals. Yes, we humans have hair on our heads and elsewhere, but compared with our relatives, even the hairiest person is basically bare.

How did we come to be so denuded? Scholars have pondered this question for centuries. Finding answers has been difficult, however: most of the hallmark transitions in human evolution—such as the emergence of upright walking—are recorded directly in the fossils of our predecessors, but none of the known remains preserves impressions of human skin. In recent years, though, researchers have realized that the fossil record does contain indirect hints about our transformation from hirsute to hairless. Thanks to these clues and insights gleaned over the past decade or so from genomics and physiology, I and others have pieced together a compelling account of why and when humans shed their fur. In addition to explaining a very peculiar quirk of our appearance, the scenario suggests that naked skin itself played a crucial role in the evolution of other characteristic human traits, including our large brain and dependence on language.

HAIRY SITUATIONS

TO UNDERSTAND WHY our ancestors lost their body hair, we must first consider why other species have coats in the first place. Hair is a type of body covering that is unique to mammals. Indeed, it is a defining characteristic of the class: all mammals possess at least some hair, and most of them have it in abundance. It provides insulation and protection against abrasion, moisture, damaging rays of sunlight, and potentially harmful parasites and microbes. It also works as camouflage to confuse predators, and its distinctive patterns allow members of the same species to

IN BRIEF

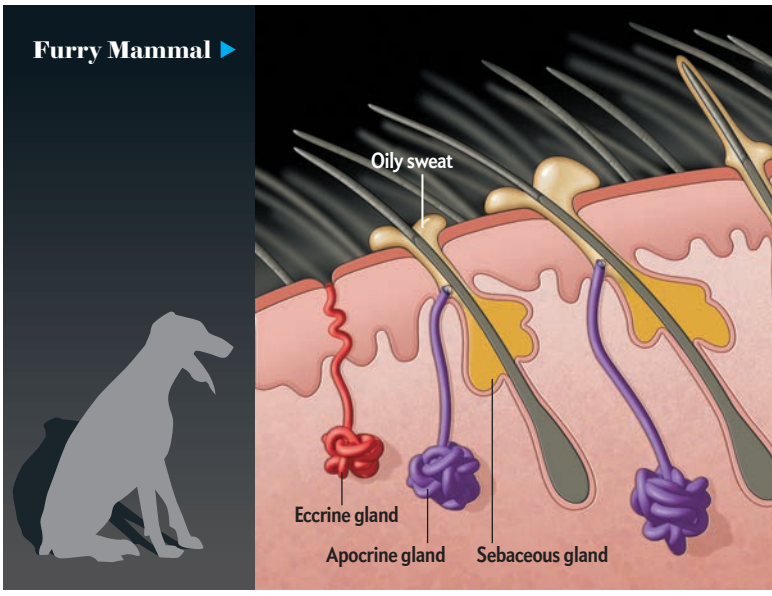
Humans are the only primate species that has mostly naked skin.
Loss of fur was an adaptation to changing environmental conditions that forced our ancestors to travel longer distances for food and water.
Analyses of fossils and genes hint at when this transformation occurred.
The evolution of hairlessness helped to set the stage for the emergence in our kind of large brains and symbolic thought.

DORIT THIS

BENEFITS OF HAIRLESSNESS

Furry vs. Naked

Naked human skin is better at ridding the body of excess heat than is fur-covered skin. Mammals possess three types of glands for the purpose: apocrine, eccrine and sebaceous. In most mammals the outermost layer of the skin, known as the epidermis, contains an abundance of apocrine glands. These glands cluster around hair follicles and coat the fur in a lather of oily sweat. Evaporation of this sweat, which cools the animal by drawing heat away from the skin, occurs at the surface of the fur. But the more the animal perspires, the less effectively it eliminates heat because the fur becomes matted, hampering evaporation. In the human epidermis, in contrast, eccrine glands predominate. These glands reside close to the skin surface and discharge thin, watery sweat through tiny pores. In addition to evaporating directly from the skin surface, this eccrine sweat vaporizes more readily than apocrine sweat, thus permitting improved cooling.



recognize one another. Furthermore, mammals can use their fur in social displays to indicate aggression or agitation: when a dog "raises its hackles" by involuntarily elevating the hairs on its neck and back, it is sending a clear signal to challengers to stay away.

Yet even though fur serves these many important purposes, a number of mammal lineages have evolved hair that is so sparse and fine as to serve no function. Many of these creatures live underground or dwell exclusively in the water. In subterranean mammals, such as the naked mole rat, hairlessness evolved as a response to living in large underground colonies, where the benefits of hair are superfluous because the animals cannot see one another in the dark and because their social structure is such that they simply huddle together for warmth. In marine mammals that never venture ashore, such as whales, naked skin facilitates long-distance swimming and diving by reducing drag on the skin's surface. To compensate for the lack of external insulation, these animals have blubber under the skin. In contrast, semiaquatic mammals—otters, for example—have dense, waterproof fur that traps air to provide positive buoyancy, thus decreasing the effort needed to float. This fur also protects their skin on land.

The largest terrestrial mammals—namely, elephants, rhinoceroses and hippopotamuses—also evolved naked skin because they are at constant risk of overheating. The larger an animal is, the less surface area it has relative to overall body mass and the harder it is for the creature to rid its body of excess heat. (On the flip side, mice and other small animals, which have a high surface-to-volume ratio, often struggle to retain sufficient heat.) During the Pleistocene epoch, which spans the time between two million and 10,000 years ago, the mammoths and other relatives of modern elephants and rhinoceroses were "woolly" because they lived in cold environments, and external insulation helped them conserve body heat and lower their food intake. But all of today's megaherbivores live in sweltering conditions, where a fur coat would be deadly for beasts of such immense proportions.

Human hairlessness is not an evolutionary adaptation to living underground or in the water—the popular embrace of the so-called aquatic ape hypothesis notwithstanding [*see box on opposite page*]. Neither is it the result of large body size. But our bare skin is related to staying cool, as our superior sweating abilities suggest.

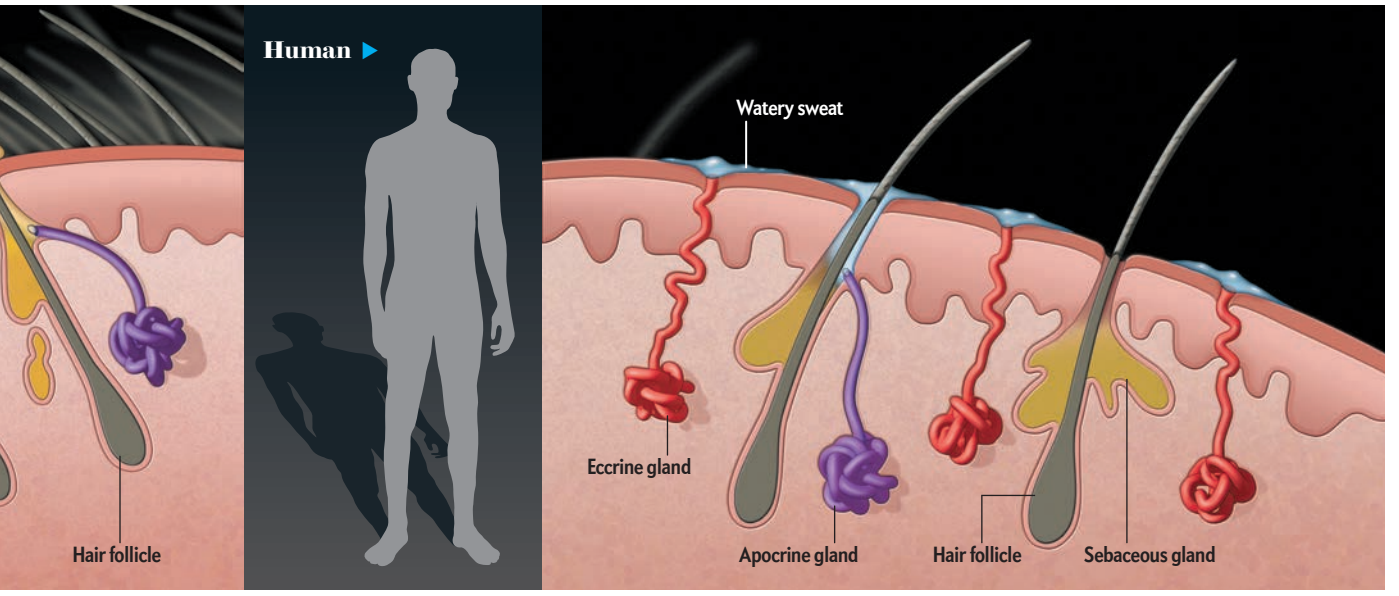
SWEATING IT OUT

KEEPING COOL IS A BIG PROBLEM for many mammals, not just the giant ones, especially when they live in hot places and generate abundant heat from prolonged walking or running. These animals must carefully regulate their core body temperature because their tissues and organs, specifically the brain, can become damaged by overheating.

Mammals employ a variety of tactics to avoid burning up: dogs pant, many cat species are most active during the cooler evening hours, and many antelopes can off-load heat from the blood in their arteries to blood in small veins that has been cooled by breathing through the nose. But for primates, including humans, sweating is the primary strategy. Sweating cools the body through the production of liquid on the skin's surface that then evaporates, drawing heat energy away from the skin in the process. This whole-body cooling mechanism operates according to the same principle as an evaporative cooler (also known as a swamp cooler), and it is highly effective in preventing the dangerous overheating of the brain, as well as of other body parts.

Not all sweat is the same, however. Mammalian skin contains three types of glands—sebaceous, apocrine and eccrine—that together produce sweat. In most species, sebaceous and apocrine glands are the dominant sweat glands and are located near the base of hair follicles. Their secretions combine to coat hairs with an oily, sometimes foamy, mixture (think of the lather a racehorse generates when it runs). This type of sweat helps to cool the animal. But its ability to dissipate heat is limited. G. Edgar Folk, Jr., of the University of Iowa and his colleagues showed more than two decades ago that the effectiveness of cooling di-

Illustration by Tami Tolpa (skin cross sections) and Jen Christiansen (dog and *human)*



minishes as an animal's coat becomes wet and matted with this thick, oily sweat. The loss of efficiency arises because evaporation occurs at the surface of the fur, not at the surface of the skin itself, thus impeding the transfer of heat. Under conditions of duress, heat transfer is inefficient, requiring that the animal drink large amounts of water, which may not be readily available. Fur-covered mammals forced to exercise energetically or for prolonged periods in the heat of day will collapse from heat exhaustion.

Humans, in addition to lacking fur, possess an extraordinary number of eccrine glands—between two million and five million—that can produce up to 12 liters of thin, watery sweat a day. Eccrine glands do not cluster near hair follicles; instead they reside relatively close to the surface of the skin and discharge sweat through tiny pores. This combination of naked skin and watery sweat that sits directly atop it rather than collecting in the fur allows humans to eliminate excess heat very efficiently. Research by Daniel E. Lieberman of Harvard University and Dennis M. Bramble of the University of Utah showed that in humans the cooling system is so superior that in a marathon, on a hot day, a human could outcompete a horse.

ALTERNATIVE IDEAS

Why the Aquatic Ape Theory Doesn't Hold Water

Among the many theories that attempt to explain the evolution of naked skin in humans, the aquatic ape theory (AAT)—which posits that humans went through an aquatic phase in their evolution—has attracted the most popular attention and support. First enunciated by English zoologist Sir Alister Hardy in a popular scientific article in 1960, the AAT later found a champion in writer Elaine Morgan, who promoted the theory in her lectures and writings before her death in 2013. The problem is, the theory is demonstrably wrong.

The AAT holds that around five million to seven million years ago tectonic upheavals in the Rift Valley of East Africa cut early human ancestors off from their preferred tropical forest environments. As a result, they had to adapt to a semiaquatic life in marshes, along coasts and in floodplains, where they lived for about a million years. Evidence of this aquatic phase, Morgan argued, comes from several anatomical features humans share with aquatic and semiaquatic mammals but not with savanna mammals. These traits include our bare skin, a reduced number of apocrine glands, and fat deposits directly under the skin.

The AAT is untenable for three major reasons. First, aquatic mammals themselves differ considerably in the degree to which they exhibit Morgan's aquatic traits. Thus, there is no simple connection between, say, the amount of hair an animal has and the environment in which it lives. Second, the fossil record shows that watery habitats were thick with hungry crocodiles and aggressive hippopotamuses. Our small, defenseless ancestors would not have stood a chance in an encounter with such creatures. Third, the AAT is overly complex. It holds that our forebears shifted from a terrestrial way of life to a semiaquatic one and then returned to living on terra firma full-time. As John H. Langdon of the University of Indianapolis has argued, a more straightforward interpretation of the fossil record is that humans always lived on land, where the driving force behind the evolution of naked skin was climate change that favored savanna grasslands over woodlands. And from a scientific perspective, the simplest explanation is usually the correct one. —*N.G.J.*

WHEN NAKEDNESS EVOLVED

Ancestors on the Move

Although the fossil record does not preserve any direct evidence of ancient human skin, scientists can estimate when nakedness evolved based on other fossil clues. Protohumans such as the australopithecines (*1*) probably led relatively sedentary lives, as today's apes do, because they lived in or near wooded environments rich in plant foods and freshwater. But as woodlands shrank and grasslands expanded, later ancestors, such as *Homo ergaster* (*2*), had to travel ever farther in search of sustenance—including meat. This species, which arose by 1.6 million years ago, was probably the first to possess naked skin and eccrine sweat, which would have offset the body heat generated by such elevated activity levels.

1 *Australopithecus afarensis*, represented here by the 3.2-million-year-old Lucy fossil, was apelike in having short legs that were not well suited to traveling long distances.

THE STORY OF US

SHOWING SOME SKIN

BECAUSE HUMANS are the only primates that lack coats and have an abundance of eccrine glands, something must have happened since our hominin lineage diverged from the line leading to our closest living relative, the chimpanzee, that favored the emergence of naked, sweaty skin. Perhaps not surprisingly, the transformation seems to have begun with climate change.

By using fossils of animals and plants to reconstruct ancient ecological conditions, scientists have determined that starting around three million years ago the earth entered into a phase of global cooling that had a drying effect in East and Central Africa, where human ancestors lived. With this decline in regular rainfall, the wooded environments favored by early hominins gave way to open savanna grasslands, and the foods that our ancestors the australopithecines subsisted on—fruits, leaves, tubers and seeds—became scarcer, more patchily distributed and subject to seasonal availability, as did permanent sources of freshwater. In response to dwindling resources, our forebears would have had to abandon their relatively leisurely foraging habits for a much more consistently active way of life just to stay hydrated and obtain enough calories, traveling ever longer distances in search of water and edible plant foods.

It is around this time that hominins also began incorporating meat into their diet, as revealed by the appearance of stone tools and butchered animal bones in the archaeological record around 2.6 million years ago. Animal foods are considerably richer in calories than are plant foods, but they are rarer on the landscape. Carnivorous animals therefore need to range farther and wider than their herbivorous counterparts to procure a sufficient amount of food. Prey animals are also moving targets, save for the occasional carcass, which means predators must expend that much more energy to obtain their meal. In the case of human hunters and scavengers, natural selection morphed the apelike proportions of the australopithecines, who still spent some time in the trees, into a long-legged body built for sustained striding and running. (This modern form also no doubt helped our ancestors avoid becoming dinner themselves when out in the open.)

But these elevated activity levels came at a price: a greatly increased risk of overheating. Beginning in the 1980s, Peter Wheeler of Liverpool John Moores University in England published a series of papers in which he simulated how hot ancestral humans would have become out on the savanna. Wheeler's work, together with research my colleagues and I published in 1994, shows that the increase in walking and running, during which muscle activity builds up heat internally, would have required that hominins both enhance their eccrine sweating ability and lose their body hair to avoid overheating.

When did this metamorphosis occur? Although the human fossil record does not preserve skin, researchers do have a rough idea of when our forebears began engaging in modern patterns of movement. Studies conducted independently by Lieberman and Christopher Ruff of Johns Hopkins University have shown that by about 1.6 million years ago an early member of our genus called *Homo ergaster* had evolved essentially modern body proportions, which would have permitted prolonged walking and running. Moreover, details of the joint surfaces of the ankle, knee and hip make clear that these hominins actually exerted themselves in this way. Thus, according to the fossil evidence, the transition to naked skin and an eccrine-based sweating system must have been well under way by 1.6 million years ago to offset the greater heat loads that accompanied our predecessors' newly strenuous way of life.

DENIS FINNIN AND JACKIE BECKETT *American Museum of Natural History* (1 and 2)

Illustrations by Victor Deak

2 ***Homo ergaster*** **was the first hominin to possess long, striding legs, seen here in the 1.6-million-year-old Turkana Boy skeleton. Such elongated limbs facilitated sustained walking and running.**

Another clue to when hominins evolved naked skin has come from investigations into the genetics of skin color. In an ingenious study, Alan R. Rogers of the University of Utah and his colleagues examined sequences of the human *MC1R* gene, which is among the genes responsible for producing skin pigmentation. The team showed that a specific gene variant always found in Africans with dark pigmentation originated as many as 1.2 million years ago. Early human ancestors are believed to have had pinkish skin covered with black fur, much as chimpanzees do, so the evolution of permanently dark skin was presumably a requisite evolutionary follow-up to the loss of our sun-shielding body hair. Rogers's estimate thus provides a minimum age for the dawn of nakedness.

SKIN DEEP

LESS CERTAIN THAN WHY and when we became naked is how hominins evolved bare flesh. The genetic evidence for the evolution of nakedness has been difficult to locate because many genes contribute to the appearance and function of our skin. Nevertheless, hints have emerged from large-scale comparisons of the sequences of DNA "code letters," or nucleotides, in the entire genomes of different organisms. Comparison of the human and chimp genomes reveals that one of the most significant differences between chimp DNA and our own lies in the genes that code for proteins that control properties of the skin. The human versions of some of those genes encode proteins that help to make our skin particularly waterproof and scuff-resistant—critical properties, given the absence of protective fur. This finding implies that the advent of those gene variants contributed to the origin of nakedness by mitigating its consequences.

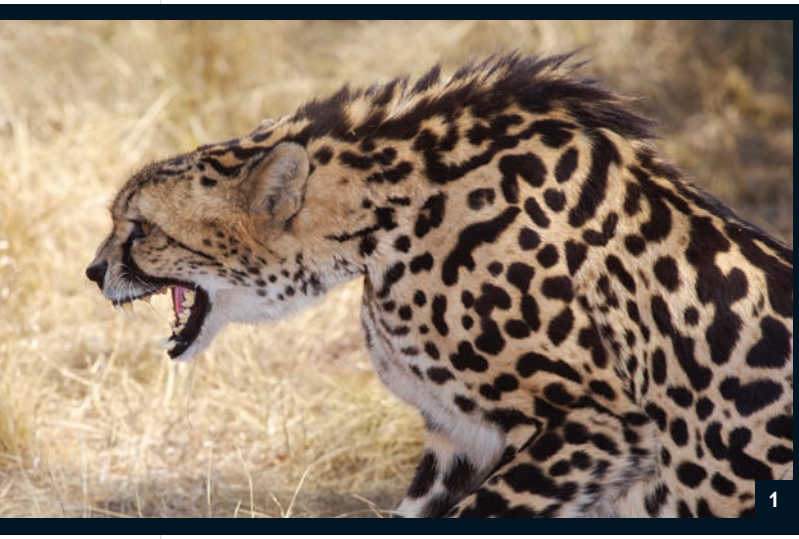
The outstanding barrier capabilities of our skin arise from the structure and makeup of its outermost layer, the stratum corneum (SC) of the epidermis. The SC has what has been described as a bricks-and-mortar composition. In this arrangement, multiple layers of flattened dead cells called corneocytes, which contain the protein keratin and other substances, are the bricks; ultrathin layers of lipids surrounding each of the corneocytes make up the mortar.

Most of the genes that direct the development of the SC are ancient, and their sequences are highly conserved among vertebrates. That the genes undergirding the human SC are so distinctive signifies, therefore, that the advent of those genes was important to survival. These genes encode the production of a unique combination of proteins that occur only in the epider-

Beating the Heat

Naked skin is not the only adaptation humans evolved to maintain a healthy body temperature in the sweltering tropics where our ancestors lived. They also developed longer limbs, increasing their surface-to-volume ratio, which in turn facilitated the loss of excess heat. That trend seems to be continuing even today. The best evidence of this sustained adaptation comes from populations in East Africa, such as the Dinka of southern Sudan. It is surely no coincidence that these people, who live in one of the hottest places on earth, also have extremely long limbs.

Why do modern humans exhibit such a wide range of limb proportions? As our forebears migrated out of tropical Africa into cooler parts of the world, the selection pressures changed, allowing for a variety of body shapes to evolve.



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SOCIAL SIGNALING is an important function of fur—from raised hackles indicating aggression to coat patterns that help members of the same species to recognize one another (*1*). We humans compensate for our lack of fur by decorating our bodies with tattoos (*2*), jewelry and other adornments. We also have complex facial expressions (*3*), as well as the ability to convey our emotions through language (*4*).

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mis, including novel types of keratin and involucrin. A number of laboratories are currently attempting to unravel the precise mechanisms responsible for regulating the manufacture of these proteins.

Other researchers are looking at the evolution of keratins in body hair, with the aim of determining the mechanisms responsible for the sparseness and fineness of body hair on the surface of human skin. Roland Moll of Philipps University in Marburg, Germany, and his colleagues have shown that the keratins present in human body hair are extremely fragile, which is why these hairs break so easily compared with those of other animals. This finding suggests that human hair keratins were not as important to survival as the hair keratins of other primates were over the course of evolution and thus became weak.

Another question geneticists are eager to answer is how human skin came to contain such an abundance of eccrine glands. Almost certainly this accumulation occurred through changes in the genes that determine the fate of epidermal stem cells, which are unspecialized, in the embryo. Early in development, groups of epidermal stem cells in specific locations interact with cells of the underlying dermis, and genetically driven chemical signals within these niches direct the differentiation of the stem cells into hair follicles, eccrine glands, apocrine glands, sebaceous glands or plain epidermis. Many research groups are now investigating how epidermal stem cell niches are established and maintained, and this work should clarify what directs the fate of embryonic epidermal cells and how more of these cells become eccrine sweat glands in humans. Intriguing progress was made in 2013 by a group led by Pardis C. Sabeti of Harvard University. The team demonstrated that a variant of a gene for the ectodysplasin receptor—a protein crucial for the formation of skin, hair, nails, teeth and sweat glands—may be associated with higher densities of eccrine sweat glands in some human populations.

Of Lice and Men

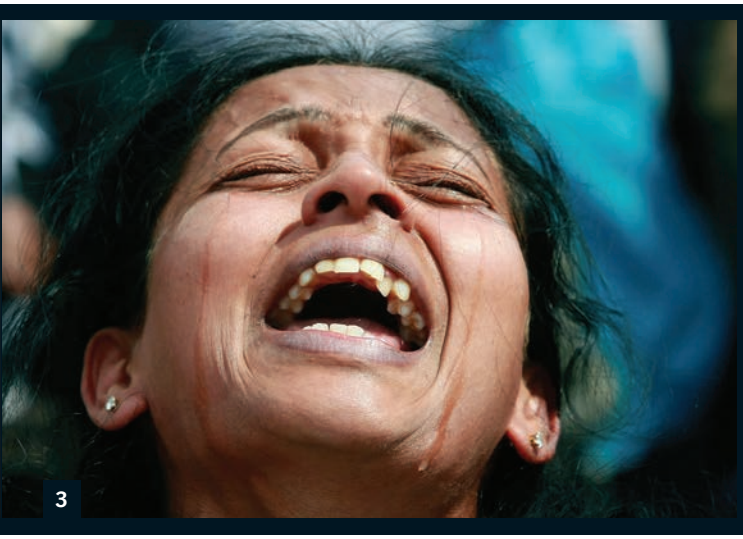
Researchers have looked to lice for clues to why humans lost their body hair. In 2003 Mark Pagel of the University of Reading in England and Walter Bodmer of John Radcliffe Hospital in Oxford proposed that humans shed their fur to rid their bodies of disease-spreading lice and other fur-dwelling parasites and to advertise the health of their skin. Other investigators have studied head and body lice for insight into how long after becoming bare-skinned our ancestors began to cover up with clothing.

Although body lice feed on blood, they live on clothing. Thus, the origin of body lice provides a minimum estimate for the dawn of hominin garb. By comparing gene sequences of organisms, investigators can learn roughly when the species arose. Such analyses in lice indicate that whereas head lice have plagued humans from the start, body lice evolved much later. The timing of their appearance hints that humans went naked for more than a million years before getting dressed.

NOT ENTIRELY NUDE

HOWEVER IT WAS THAT we became naked apes, evolution did leave a few body parts covered. Any explanation of why humans lost their fur therefore must also account for why we retain it in some places. Hair in the armpits and groin probably serves both to propagate pheromones (chemicals that serve to elicit a behavioral response from other individuals) and to help keep these areas lubricated during locomotion. As for hair on the head, it was most likely retained to help shield against excess heat on the top of the head. That notion may sound paradoxical, but having dense hair on the head creates a barrier layer of air between the sweating scalp and the hot surface of the hair. Thus, on a hot, sunny day the hair absorbs the heat while the barrier layer of air remains cooler, allowing sweat on the scalp to evaporate into that layer of air. Tightly curled hair provides the optimum head covering in this regard because it increases the thickness of the space between the surface of the hair and the scalp, allowing air to blow through. Much remains to be discovered about the evo-

HEINRICH VAN DEN BERG *Getty Images (1)*; HENRY HORNSTEIN *Getty Images (2)*



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lution of human head hair, but it is possible that tightly curled hair was the original condition in modern humans and that other hair types evolved as humans dispersed out of tropical Africa.

With regard to our body hair, the question is why it is so variable. There are many populations whose members have hardly any body hair at all and some populations of hirsute folks. Those with the least body hair tend to live in the tropics, whereas those with the most tend to live outside the tropics. Yet the hair on these nontropical people provides no warmth to speak of. These differences in hairiness clearly stem to some extent from testosterone because males in all populations have more body hair than females do. A number of theories aimed at explaining this imbalance attribute it to sexual selection. For example, one posits that females prefer males with fuller beards and thicker body hair because these traits occur in tandem with virility and strength. Another proposes that males have evolved a preference for females with more juvenile features. These are interesting hypotheses, but no one has actually tested them in a modern human population. In the absence of any empirical evidence, it is still anybody's guess why human body hair varies the way it does.

NAKED AMBITIONS

GOING FURLESS WAS NOT merely a means to an end; it had profound consequences for subsequent phases of human evolution. The loss of most of our body hair and the gain of the ability to dissipate excess body heat through eccrine sweating helped to make possible the dramatic enlargement of our most temperature-sensitive organ, the brain. Whereas the australopithecines had a brain that was, on average, 400 cubic centimeters—roughly the size of a chimp's brain—*H. ergaster* had a brain twice that large. And within a million years the human brain swelled another 400 cubic centimeters, reaching its modern size. No doubt other factors influenced the expansion of our gray matter—the adoption of a sufficiently caloric diet to fuel this energetically demanding tissue, for example. But shedding our body hair was surely a critical step in becoming brainy.

Our hairlessness also had social repercussions. Although we can technically raise and lower our hackles when the small muscles at the base of our hair follicles contract and relax, our body hairs are so thin and wispy that we do not put on much of a show compared with the displays of our cats and dogs or of our chimpanzee cousins. Neither do we have the built-in advertising—or camouflage—offered by zebra stripes, leopard spots, and the like. Indeed, one might even speculate that universal human traits such as social blushing and complex facial expressions evolved to compensate for our lost ability to communicate through our fur. Likewise, body paint, cosmetics, tattoos and other types of skin decoration are found in various combinations in all cultures because they convey group membership, status and other vital social information formerly encoded by fur. We also employ body postures and gestures to broadcast our emotional states and intentions. And we use language to speak our mind in detail. Viewed this way, naked skin did not just cool us down—it helped make us who we are. SA

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MORE TO EXPLORE

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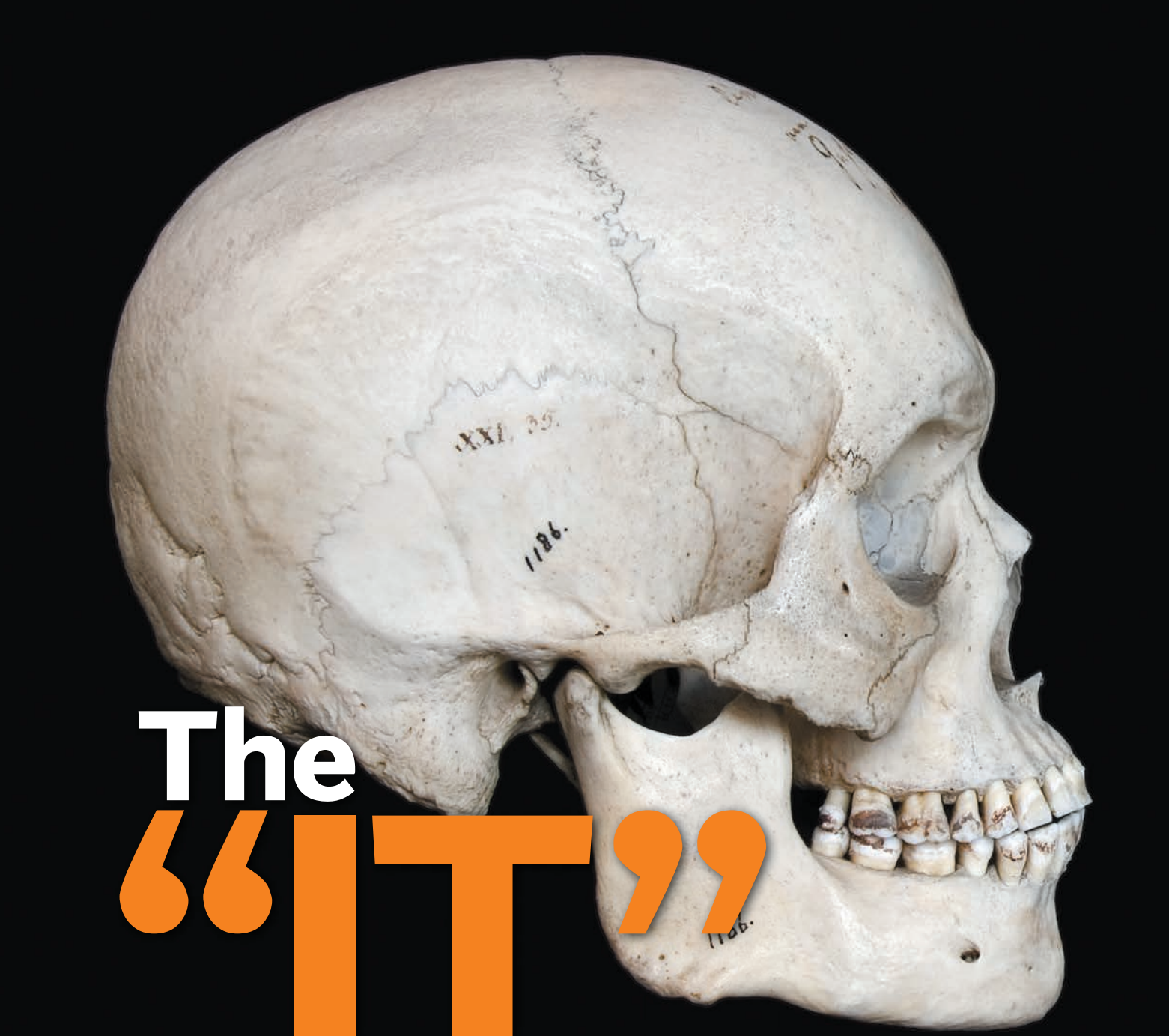


The "IT" Factor

The capacity to engage in shared tasks such as hunting large game and building cities may be what separated modern humans from our primate cousins

By Gary Stix

SKULL OF A HUMAN faces off with a chimpanzee skull (*at right*). Despite divergent brain sizes, chimps have many of the same cognitive abilities as humans, with a few key exceptions.

AT A PSYCHOLOGY LABORATORY IN LEIPZIG, GERMANY, TWO TODDLERS eye gummy bears that lie on a board beyond their reach. To get the treats, both tots must pull in tandem on either end of a rope. If only one child pulls, the rope detaches, and they wind up with nothing. A few miles away, in a plexiglass enclosure at Pongoland, the ape facility at the Leipzig Zoo, researchers repeat the identical experiment, but this time with two chimpanzees. If the primates pass the rope-and-board test, each one gets a fruit treat. By testing children and chimps in this way, investigators hope to solve a vexing puzzle: Why are humans so successful as a species? *Homo sapiens* and *Pan troglodytes* share almost 99 percent of their genetic material. Why, then, did humans come to populate virtually every corner of the planet—building the Eiffel Tower, Boeing 747s and H-bombs along the way? And why are chimps still foraging for their supper in the dense forests of equatorial Africa, just as their ancestors did seven or so million years ago, when archaic humans and the great apes separated into different species?

As with any event that occurred on the timescale of evolution—hundreds of thousands or millions of years in the making—scientists may never reach a consensus on what really happened. For years the prevailing view was that only humans make and use tools and are capable of reasoning using numbers and other symbols. But that idea fell by the wayside as we learned more about what other primates are capable of. A chimp, with the right coach, can add numbers, operate a computer and light up a cigarette.

At present, the question of why human behavior differs from that of the great apes, and how much, is still a matter of debate. Yet experiments such as the one in Leipzig, under the auspices of the Max Planck Institute for Evolutionary Anthropology, have revealed a compelling possibility, identifying what may be a unique, but easy to overlook, facet of the human cognitive apparatus. From before their first birthday—a milestone some psychologists term "the nine-month revolution"—children begin to show an acute awareness of what goes on inside their mother's and father's heads. They evince this new ability by following their parents' gaze or looking where they point. Chimps can also figure out what is going on in a companion's mind to some degree, but humans take it one step further: infant and elder also have the ability to put their heads together to focus on what must be done to carry out a shared task. The simple act of adult and infant rolling a ball back and forth is enabled by this subtle cognitive advantage.

Some psychologists and anthropologists think that this melding of minds may have been a pivotal skill that arose hundreds of thousands of years ago and that shaped later human evolution. The ability of small bands of hunter-gatherers to work together in harmony ultimately set off a cascade of cognitive changes that led to the development of language and the spread of diverse human cultures across the globe.

This account of human psychological evolution, synthesized from bits and pieces of research on children and chimps, is speculative, and it has its doubters. But it provides perhaps the most impressively broad-ranging picture of the origins of cognitive abilities that make humans special.

THE RATCHET EFFECT

THE MAX PLANCK INSTITUTE maintains the world's largest research facility devoted to examining the differences in behavior between humans and the great apes. Dozens of studies may be running at any one time. Researchers can draw subjects from a database of more than 20,000 children and recruit chimpanzees or members of any of the other great ape species—orangutans, bonobos and gorillas—from the Wolfgang Köhler Primate Research Center at the Leipzig Zoo a few miles away.

One institute researcher is Michael Tomasello, a tall, bearded psychologist and primatologist. He grew up in a small citrus-growing city at the epicenter of the Florida peninsula. He began his academic career at the University of Georgia with a dissertation on the way toddlers acquire language. While he was doing his doctorate in the 1970s, linguists and psychologists often cited language as exhibit number one for human exceptionalism in the animal world.

Tomasello's doctoral thesis chronicled how his almost two-year-old daughter learned her first verbs. The emergence of proto words—"play play" or "ni ni"—revealed a natural inclination of the young child to engage in trial-and-error testing of language elements, an exercise that gradually took on the more conventional structuring of grammar and syntax. This learning process stood in contrast to the ideas of Noam Chomsky and other linguists who contended that grammar is somehow genetically hardwired in our brains—an explanation that struck Tomasello as reductionist. "Language is such a complicated thing that it couldn't have evolved like the opposable thumb," he says.

His work on language broadened his thinking about the relation between culture and human evolution. Tomasello realized that selective forces alone, acting on physical traits, could not explain the emergence of complex tools, language, mathematics and elaborate social institutions in the comparatively brief interval on the evolutionary time line since humans and chimps parted ways. Some innate mental capacity displayed by hominins (modern humans and our extinct relatives) but absent in nonhuman primates must have enabled our forebears to behave in ways that vastly hastened the ability to feed and clothe themselves and to flourish in any environment, no matter how forbidding.

When Tomasello moved to a professorship at Emory University during the 1980s, he availed himself of the university's Yerkes primate research center to look for signs of this capacity in studies comparing the behaviors of children with those of chimps. The move set in motion a multidecade quest that he has continued at Max Planck since 1998.

In his studies of chimp learning, Tomasello noticed that apes do not ape each other the way humans imitate one another. One chimp might emulate another chimp using a stick to fetch ants out of a nest. Then others in the group might do the same. As Tomasello looked more closely, he surmised that chimps were able to understand that a stick could be used for "ant dipping," but they were unconcerned with mimicking one technique or another that might be used in hunting for the insects. More important, there was no attempt to go beyond the basics and then do some tinkering to make a new and improved ant catcher.

In human societies, in contrast, this type of innovation is a distinguishing characteristic that Tomasello describes as a "ratchet effect." Humans modify their tools to make them better and then pass this knowledge along to their descendants, who make their own tweaks—and the improvements ratchet up. What starts as a lobbed stone projectile invented to kill a mammoth evolves over the millennia into a slingshot and then a catapult, a bullet, and finally an intercontinental ballistic missile.

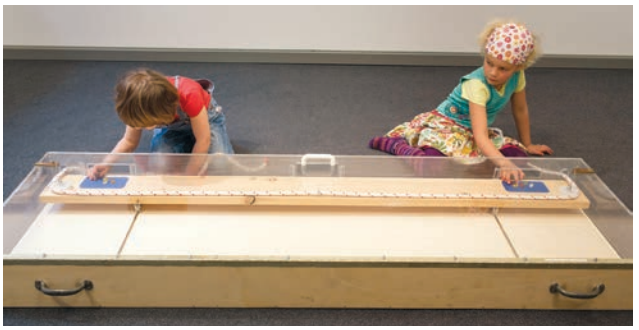
IN BRIEF

Humans—it was once thought—differed from other animals by their use of tools and their overall superiority in a range of cognitive abilities. Close observation of the behaviors of chimpanzees and other great apes has proved these ideas to be wrong.

Chimpanzees score as highly as young children on tests of general reasoning abilities but lack many of the social skills that come naturally to their human cousins. Unlike humans, chimps do not collaborate in the large groups needed to build complex societies.

Comparison of human and chimp psychology reveals that an essential source of the differences in humans may be the evolution of the ability to intuit what another person is thinking so that both can work toward a shared goal.

PRECEDING PAGES: INGO ARNDT *Getty Images*



EYES ON THE PRIZE: Both children and chimpanzees sometimes undergo the same tests to compare how closely members of each species work with one another. The two partners must cooperate by pulling each rope in unison to get a treat—either gummy bears in a child laboratory at the Max Planck Institute or bananas or other fruit at the nearby zoo. If one team member pulls and the other does not, the rope comes free, and the pair go hungry.

This cultural ratchet provides a rough explanation for humans' success as a species but leads to another question: What specific mental processes were involved in transmitting such knowledge to others? The answer has to begin with speculations about changes in hominin physiology and behavior that may have taken place hundreds of thousands of years ago. One idea—the social brain hypothesis, put forward by anthropologist Robin Dunbar of the University of Oxford—holds that group size, and hence cultural complexity, scales up as brains get bigger. And scientists know that by 400,000 years ago, *Homo heidelbergensis,* probably our direct ancestor, had a brain almost as large as ours.

Tomasello postulates that, equipped with a bigger brain and confronted with the need to feed a growing population, early hominins began careful strategizing to track and outwit game. The circumstances exerted strong selection pressures for cooperation: any member of a hunting party who was not a team player—taking on a carefully defined role when tracking and cornering an animal—would have been excluded from future outings and so might face an unremittingly bleak future. If one hunter was a bad partner, Tomasello notes, the rest of the group would then decide: "We won't do this again." In his view, what separated modern humans from the hominin pack was an evolutionary adaptation for hypersociality.

The paleoarchaeological record of bones and artifacts is too scant to provide support for Tomasello's hypothesis. He draws his evidence from a comparison of child and chimp—matching our closest primate relative with a toddler who has yet to master a language or be exposed to formal schooling. The untutored child allows researchers to assess cognitive skills that have yet to be fully shaped by cultural influences and so can be considered to be innate.

Studies in Leipzig during the past decade or so have uncovered more similarities than differences between humans and chimps, but they also highlight what Tomasello calls "a small difference that made a big difference." One immense research undertaking, led by Esther Herrmann of the developmental and comparative psychology department at the Max Planck Institute under Tomasello's tutelage, ran from 2003 until its publication in *Science* in 2007. It entailed administering multiple cognitive tests to 106 chimpanzees at two African wildlife sanctuaries, 32 orangutans in Indonesia and 105 toddlers, aged two and a half years, in Leipzig.

The investigators set out to determine whether humans' bigger brain meant the children were smarter than great apes and, if so, what being smarter meant, exactly. The three species were tested on spatial reasoning (such as looking for a hidden reward), an ability to discriminate whether quantities were large or small, and an understanding of cause-and-effect relationships. It turned out that the toddlers and the chimpanzees scored almost identically on these tests (orangutans did not perform quite as well).

When it came to social skills, though, there was no contest. Toddlers bested both chimps and orangutans on tests (adapted for nonverbal apes) that examined the ability to communicate, learn from others, and evaluate another being's perceptions and wishes. The researchers interpreted the results as showing that human children are not born with a higher IQ (general reasoning capacities) but rather come equipped with a special set of abilities—"cultural intelligence," as the *Science* study put it—that prepares them for learning later from parents, teachers and playmates. "It was really the first time that it was shown that social-cognitive abilities are the key skills that make us special in comparison to other animals," Herrmann says.

Digging deeper required probing for the specific psychological processes that underlie humans' ultrasocial tendencies. Tomasello's research showed that at about nine months of age, parent and child engage in a figurative form of mind reading. Each has what psychologists call a "theory of mind." Each is aware of what the other one knows when they look together at a ball or block and play a little game with it. Each carries a mental image of these items in the same way a group of *H. heidelbergensis* would have all visualized a deer intended as dinner. This capacity to engage with another person to play a game or achieve a common goal is what Tomasello calls shared intentionality (a term he borrowed from philosophy). In Tomasello's view, shared intentionality is an evolutionary adaptation unique to humans—a minute difference with momentous consequences, rooted in an inherited predisposition for a degree of cooperative social interactions that is absent in chimps or any other species.

THE BENEFITS OF MIND READING

THE INSTITUTE RESEARCHERS NOTED that chimps, too, can read one another's minds to some degree. But their natural inclination is to use whatever they learn in that way to outcompete one another in the quest for food or mates. The chimp mind, it appears, is involved in a kind of Machiavellian mental scheming—"If I do this, will he do that?"—as Tomasello explains it. "It is inconceivable," he said in an October 2010 talk at the University of Virginia, "that you would ever see two chimpanzees carrying a log together."

Photographs by Daniel Rosenthal

The Leipzig researchers formally demonstrated the differences that separate the two species in the rope-and-board experiment in which two chimpanzees at the Leipzig Zoo could get a snack of fruit only if they both pulled a rope attached to a board. If food was placed at both ends of the board, the apes took the fruit closest to them. If the treats were placed in the middle, however, the more dominant ape would grab the food, and after a few trials, the subordinate simply stopped playing. In the institute's child lab, the children worked together, whether the gummy bears were placed in the middle or at the ends of the board. When the treat was in the middle, the three-year-olds negotiated so that each would get an equal share.

Ancestral humans' mutual understanding of what was needed to get the job done laid the basis for the beginnings of social interactions and a culture based on cooperation, Tomasello argues. This "common ground," as he calls it, in which members of a group know much of what others know, may have opened the way for development of new forms of communication.

An ability to devise and perceive shared goals—and to intuit immediately what a hunting partner was thinking—apparently allowed our hominin ancestors to make cognitive strides in other ways, such as developing more sophistication in communicative uses of gesturing than our ape relatives possess.

The basic gestural repertoire of our hominin kin may have once been similar to that of the great apes. Archaic humans may have pointed, as chimpanzees do today, to convey commands—"Give me this" or "Do that"—a form of communication centered on an individual's needs. Chimps, perhaps reminiscent of humans in a primeval past, still make no attempt to use these gestures for teaching or passing along information.

For humans, gesturing took on new meaning as their mental-processing abilities got better. A hunter would point to a glade in the forest to indicate where a deer was grazing, an action immediately understood by a nearby companion. The way such pointing can take on new meanings is evident in modern life. "If I point to indicate 'Let's go have a cup of coffee over there,' it's not in the language," Tomasello says. "The meaning of 'that café' is in the finger, not in the language."

Young children understand this type of pointing, but chimps do not. This difference became evident in one study in which the experimenter repeatedly put blocks on a plate that the child needed for building a tower, which the child then used. At a certain juncture, there were no objects left when needed, and so the infant started pointing to the now empty plate, indicating that she wanted one of the blocks that were no longer there. The child knew that the adult would make the correct inference—the ability to refer to an absent entity is, in fact, a defining characteristic of human language. At the zoo, chimps put through a similar exercise—with food substituted for blocks—did not lift a finger when facing a vacant plate. Only slightly older children start to understand gestures that pantomime an action—moving a hand to one's mouth to represent hunger or thirst. Chimps seeing these gestures during a study remain clueless. An ape will understand what is happening when a human applies a hammer to a nut to get the meat but is befuddled when that same person makes a pounding motion on the hand to convey the idea of carrying out the same action.

This type of gesturing—an extension of humans' cognitive capacity for shared intentionality—may have been the basis for communicating abstract ideas needed to establish more elaborate social groups, whether they be a tribe or a nation. Pantomiming would have enabled people to create story lines, such as conveying "the antelope grazes on the other side of the hill" by holding both hands in a V shape on the top of one's head to signify the animal and then raising and lowering the hands to depict the hill. These scenarios derive from comparative experiments demonstrating that toddlers have an intuitive understanding of iconic gestures for many familiar activities but that chimpanzees do not.

Some of this gesturing occurred perhaps not just through moving the hands but also through vocalizations intended to represent specific objects or actions. These guttural noises may have evolved into speech, further enhancing the ability to manage complex social relationships as populations continued to grow—and rivalries arose among tribal groups. A group adept at working together would outcompete those that bickered among themselves.

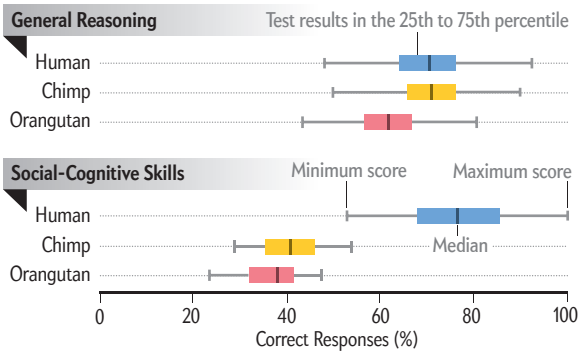
Humans' expanding cognitive powers may have promoted specific practices for hunting, fishing, plant gathering or marriage that turned into cultural conventions—the way "we" do things—that the group as a whole was expected to adopt. A collection of social norms required each individual to gain awareness of the values shared by the group—a "group-mindedness" in which every member conformed to an expected role. Social norms produced a set of moral principles that eventually laid a foundation for an institutional framework—governments, armies, legal and religious systems—to enforce the rules by which people live. The millennial journey that began with a particular mind-set needed by bands of hunters now scaled up to entire societies.

Chimps and other great apes never got started down this path. When chimps hunt together to prey on colobus monkeys in Ivory Coast, this activity, as Tomasello interprets it, entails every chimp trying to run down the monkey first to get the most meat, whereas human hunter-gatherers, even in contemporary settings, cooperate closely as they track game and later share the spoils equitably.

CROSS-SPECIES IQ TESTING

Smart as a Chimp?

One widely held hypothesis suggests that overall humans are more intelligent than other primates. A study by the Leipzig researchers showed that chimps and young children (though not orangutans) perform equally on tests of capacities measured by conventional IQ tests (*top*), such as spatial and quantitative abilities. But children do better on cognitive tests related to social skills, such as learning from others (*bottom*).



SOURCE: "HUMANS HAVE EVOLVED SPECIALIZED SKILLS OF SOCIAL COGNITION: THE CULTURAL INTELLIGENCE HYPOTHESIS," BY ESTHER HERRMANN ET AL., IN *SCIENCE*, VOL. 317; SEPTEMBER 7, 2007

Tomasello concludes that ape societies and those of other foragers such as lions may appear to cooperate, but the dynamics at play within the group are still fundamentally competitive in nature.

THE GREAT DEBATE

TOMASELLO'S VERSION of an evolutionary history is not universally accepted, even within the institution. One floor up from his office, in the department of primatology, Catherine Crockford talks me though a video her graduate student Liran Samuni made. It shows a young chimpanzee in the Taï National Park in Ivory Coast near the Liberian border.

The chimp the researchers call Shogun has just caught a large, black-and-white colobus monkey. Shogun is having trouble eating his still alive and squirming catch and issues a series of sharp "recruitment screams" to summon help from two elder hunters lodged in the tree canopy. Kuba, one of the two, arrives on the scene shortly, and Shogun calms down a bit and takes his first real bite. But then Shogun continues to scream until the other hunter, Ibrahim, shows up. The younger ape puts his finger in Ibrahim's mouth as a "reassurance gesture," a mannerism that ensures that all is well. Ibrahim gives the sought-for emotional support by not biting Shogun's finger. The three then share the meal. "It's interesting that he's recruiting these two dominant males that could take this whole monkey from him," Crockford says. "But as you can see, they're not taking it from him. He's still allowed to eat it."

Crockford argues that it is still too early to draw conclusions about the extent to which chimps cooperate. "I don't think we know the limits of what chimps are doing," she says. "I think [Tomasello's] arguments are brilliant and really clear in terms of our current knowledge, but I think that with new tools that we're taking to the field, we'll find out whether the current limits are the limits of what chimps can do or not." Working with colleagues, Crockford has developed tests that measure the social-bonding hormone oxytocin in chimpanzee urine. Their studies have shown that the hormone rises when chimps share food, a sign that the animals may cooperate when feeding.

Crockford did her doctoral studies at the institute in Leipzig, with both Tomasello and Christophe Boesch, head of the Max Planck Institute's department of primatology. Boesch has argued against Tomasello's conclusions by highlighting his own extensive research in the Taï National Park showing that chimps have a highly collaborative social structure—one chimp steers the monkey prey in the desired direction; others block its path along the way or take on yet additional roles. Boesch's views on chimp cooperation are similar to those of Frans de Waal of the Yerkes National Primate Research Center at Emory. Still others criticize Tomasello from a diametrically opposing viewpoint. Daniel Povinelli of the University of Louisiana at Lafayette contends that Tomasello overstates chimps' cognitive capacities in suggesting that they have some ability to understand the psychological state of others in the group.

For his part, Tomasello seems to enjoy being in the midst of this academic jousting, saying: "In my mind, Boesch and de Waal are anthropomorphizing apes, and Povinelli is treating them like rats, and they're neither." He adds, jokingly, "We're in the middle. Since we're getting attacked equally from both sides, we must be right."

Condemnation from some quarters is tempered by a deep respect from others. "I used to think that humans were very similar to chimps," says Jonathan Haidt, a leading social scientist at the New York University Stern School of Business. "Over the years, thanks in large part to Tomasello's work, I've come to believe that the small difference he has studied and publicized—the uniquely human ability to do shared intentionality—took us over the river to a new shore, where social life is radically different."

Resolving these debates will require more research from zoo, lab and field station—perhaps through new studies on the extent to which chimps have a theory of mind about others. Still other research already under way by Tomasello's group is intended to determine whether the conclusions about human behavior, drawn from tests on German children, carry over if similar tests are performed on children in Africa or Asia. One study asks whether German preschoolers share their collective sense of what is right or wrong with the Samburu, a seminomadic people in northern Kenya.

There may also be room to look more deeply at human-ape differences. One of Tomasello's close longtime colleagues, Josep Call, who heads the Wolfgang Köhler Center, thinks that shared intentionality alone may not suffice to explain what makes humans special. Other cognitive capacities, he says, may also differentiate humans from other primates—one example may be "mental time travel"—our ability to imagine what may happen in the future.

More perspective on the overlap between humans and chimps may come from looking inside the human brain—an endeavor that is ongoing on yet another floor at Max Planck. Svante Pääbo, who led a team that finished an initial sequencing of the Neandertal genome in 2010, conjectures in a 2014 book that Tomasello's ideas about the uniqueness of human thinking may ultimately be tested through genetic analyses.

A logical place to start would be to fuse research on chimp and human behaviors with the quixotic journey to understand the interactions among the hundreds of genes involved in autism. Children with the disorder, not unlike chimps, have difficulty understanding social cues. Comparing the genes in children with autism with those in unaffected children—and then with the DNA of chimps and perhaps even Neandertals, our closest evolutionary cousins—may yield a better understanding of a genetic basis for human sociality.

These investigations may also help explain why, over millennia, we progressed from bands of foragers to societies that not only provide food and shelter more efficiently than chimps do but also offer unceasing opportunities for social dealings—chances to move to any corner of the planet within a day's time or to convey messages to Tucson or Timbuktu as fast as a thought comes to mind. SA

Gary Stix is a senior editor at *Scientific American* and editor at large at *Scientific American Mind*.

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Neanderthal Split

Analyses of anatomy, DNA and cultural remains have yielded tantalizing insights into the inner lives of our mysterious extinct cousins

By Kate Wong

IN BRIEF

The long-standing view of Neandertals, our closest relatives, holds that they lagged far behind anatomically modern *Homo sapiens* in cognitive ability.

Studies show that they did differ from *H. sapiens* in their brain anatomy and DNA, but the functional significance of these differences is unclear.

Cultural remains provide clearer insights into the Neandertal mind—and narrow the supposed mental gap between them and us.

The findings suggest that factors unrelated to intelligence drove Neandertals to extinction while *H. sapiens* managed to flourish.

Illustration by Giordano Polini

ON A CLEAR DAY IN GIBRALTAR, LOOKING OUT OF GORHAM'S CAVE, YOU CAN see the rugged northern coast of Morocco looming purple above the turquoise sea. Inside the cave, quiet prevails, save for the lapping of waves against its rocky beach. But offshore, the strait separating this southernmost tip of the Iberian Peninsula from the African continent bustles with activity. Fishing vessels troll the waters for tuna and marlin, cruise ships carry tourists gawking at Gibraltar's hulking limestone massif, and tankers ferry crude oil from the Mediterranean to points west. With its swift, nutrient-rich currents, mild climate and gateway location, the area has attracted humans for millennia.

One impressive group dwelled in the region for tens of thousands of years, weathering several ice ages here. During such times lower sea levels exposed a vast coastal plain in front of the cave, land that supported a variety of animals and plants. These individuals cleverly exploited the local bounty. They hunted large animals such as ibex and seals and small ones such as rabbits and pigeons; they fished for bream and gathered mussels and limpets from the distant shore; they harvested pine nuts from the surrounding evergreens. Sometimes they took ravens and eagles for their plumage to bedeck themselves with the beautiful black flight feathers. And they engraved their cave floor with symbols whose meaning has since been lost to time.

In all these ways, these people behaved just like our own *Homo sapiens* ancestors, who arose in Africa with the same anatomy we have today and later colonized every corner of the globe. But they were not these anatomically modern *humans*. They were Neandertals, our stocky, heavy-browed cousins, known to have lived in Eurasia between 350,000 and 39,000 years ago—those same Neandertals whose name has come to be synonymous in pop culture with idiocy and brutishness.

The scientific basis for that popular pejorative view has deep roots. Back in the early 1900s the discovery of the first largely complete Neandertal skeleton, from the site of La Chapelle-aux-Saints in France, gave rise to the group's image problem: deformities now known to reflect the old age of the individual were seen as signs of degeneracy and subhumanness.

Since then, the pendulum of paleoanthropological opinion has swung repeatedly between researchers who see Neandertals as cognitively inferior to *H. sapiens* and those who see them as our mental equals. Now a rash of discoveries is fanning the debate. Some fossil and ancient DNA analyses seem to suggest that Neandertal brains were indeed different—and less capable—than those of *H. sapiens*. Yet mounting archaeological evidence indicates that Neandertals behaved in many of the same ways that their anatomically modern contemporaries did.

As scientists advance into the Neandertal mind, the mystery of why our closest relatives went extinct after reigning for hundreds of thousands of years is deepening. The race is on to solve this extinction riddle: such insight will help reveal what it was that distinguished our kind from the rest of the human family—and set anatomically modern humans on the path to becoming the enormously successful species we are today.

BONY INKLINGS

PALEOANTHROPOLOGISTS have long sought clues to Neandertal cognition in the fossilized skulls they left behind. By studying casts of the interior of the braincase, researchers can reconstruct the external form of an extinct human's brain, which reveals the overall size as well as the shape of certain of its regions. But those analyses have failed to turn up much in the way of clear-cut differences between Neandertal brains and those of *H. sapiens*. (Some experts think Neandertals were just another population of *H. sapiens*. This article treats the two groups as different human species, albeit very closely related ones.) Neandertal brains were a little flatter than ours, but they were just as big—indeed, in many cases they were larger, explains paleoneurologist Ralph Holloway of Columbia University. And their frontal lobes—which govern problem solving, among other tasks—were almost identical to those of *H. sapiens,* judging from the impression they left on the inside of the braincase. That impression does not reveal the internal extent or structure of those key brain regions, however. "Endocasts are the most direct evidence of brain evolution, but they are extremely limited in terms of giving you solid information about behavior," Holloway admits.

In a widely publicized study published in 2013, Eiluned Pearce of the University of Oxford and her colleagues purportedly got around some of the limitations of endocasts and provided a way of estimating the size of internal brain areas. The team used eye-socket size as a proxy for the size of the visual cortex, which is the brain region that processes visual signals. They found that the Neandertal skulls they measured had significantly larger eye sockets than modern humans have—the better for coping with the lower light levels available in their

high-latitude homes, according to one theory—and thus larger visual cortices. With more real estate dedicated to processing visual information, Neandertals would have had less neural tissue left over for other brain regions, including the ones that help us maintain extensive social networks, which can buffer against hard times, the researchers argued.

Holloway is not convinced. His own endocast work indicates that there is no way to delineate and measure the visual cortex. And Neandertal faces are larger than those of anatomically modern humans, which might explain their larger eye sockets. Moreover, people today are hugely variable in the proportion of visual cortex they have relative to other brain regions, he observes, and this anatomical variability does not appear to correspond to differences in behavior.

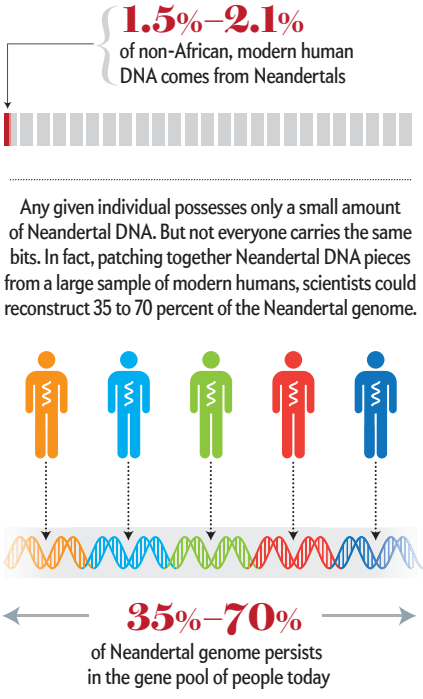
Other fossil analyses have yielded similarly equivocal signals about the Neandertal mind. Studies of limb asymmetry and wear marks on tools as well as on the teeth (from using them to grasp items such as animal hides during processing) indicate that Neandertals were as right-handed as we moderns are. A strong tendency toward favoring the right hand is one of the traits that distinguishes *H. sapiens* from chimpanzees and corresponds to asymmetries in the brain that are believed to be related to language—a key component of modern human behavior. Yet studies of skull shape in Neandertal specimens representing a range of developmental stages indicate that the Neandertals attained their large brain size through a different developmental pathway than that of *H. sapiens*. Although Neandertal brains started off growing like modern brains in the womb, they diverged from the modern growth pattern after birth, during a critical window for cognitive development.

Those developmental differences may have ancient evolutionary origins. An analysis of some 17 skulls dated to 430,000 years ago from the fossil site of Sima de los Huesos, in the Atapuerca Mountains in northern Spain, has shown that members of the population there, believed to have been Neandertal precursors, had smaller brains than later members of the lineage. The finding suggests that Neandertals did not inherit their large brain size from the last common ancestor of Neandertals and modern humans; instead the two species underwent a parallel brain expansion later in their evolution. Although Neandertal brains ended up approximately as large as ours, their independent evolution would have left plenty of opportunities for the emergence of brain differences apart from size, such as those affecting connectivity.

GENETIC RESULTS

Neandertal Legacy

Analysis of DNA recovered from several Neandertal fossils has revealed that they interbred with *Homo sapiens* after our species left Africa. Neandertal DNA lives on in many people today as a result of this long-ago mixing.


1.5%–2.1%
of non-African, modern human DNA comes from Neandertals
Any given individual possesses only a small amount of Neandertal DNA. But not everyone carries the same bits. In fact, patching together Neandertal DNA pieces from a large sample of modern humans, scientists could reconstruct 35 to 70 percent of the Neandertal genome.
35%–70%
of Neandertal genome persists in the gene pool of people today

Graphic by 5W Infographics

GENETIC HINTS

GLIMPSES OF SOME of those differences have come from DNA analyses. Since the publication of a draft of the Neandertal genome in 2010, geneticists have been mining ancient DNA to see how Neandertals and *H. sapiens* compare. Intriguingly, the Neandertals turn out to have carried a very similar variant we have of a gene called *FOXP2* that is thought to play a role in speech and language in humans. But other parts of the Neandertal genome appear to contrast with ours in significant ways. For one thing, Neandertals seem to have carried different versions of other genes involved in language, including *CNTNAP2*. Further, of the 87 genes in modern humans that differ significantly from their counterparts in Neandertals and another archaic hominin group, the Denisovans, several are involved in brain development and function.

Differences in the genetic codes of Neandertals and modern humans are not the whole story, however. The switching on and off of genes could have distinguished moderns from Neandertals, too, so that the groups differed in how robustly and under what circumstances they produced the substances encoded by their genes. Indeed, *FOXP2* itself appears to have been expressed differently in Neandertals than in *H. sapiens,* even though the protein it made was the same. Scientists have begun studying gene regulation in Neandertals and other extinct humans by examining the patterns of chemical tags known as methyl groups in ancient genomes. These tags are known to influence gene activity.

But whether or not differences in DNA sequences and gene activity translate to differences in cognition is the big question. To that end, intriguing clues have emerged from studies of people today who carry a small percentage of Neandertal DNA as a result of long-ago interbreeding between Neandertals and *H. sapiens*.

Geneticist John Blangero of the Texas Biomedical Research Institute runs a long-term study of extended families in San Antonio aimed at finding genes involved in complex diseases such as diabetes. In recent years he and his colleagues had begun looking at brain structure and function in the study participants. A biological anthropologist by training, Blangero started at one point to wonder how he could use living humans to answer such questions as what cognitive abilities Neandertals had.

A plan began to take shape. Over the course of their disease research, Blangero and his team had obtained whole-genome sequences and MRI scans of the brains of hundreds of patients. And they had developed a statistical method to gauge the effects of certain disease-linked gene variants on observable traits.

The *Homo sapiens* Effect

Neandertals ruled Eurasia for hundreds of thousands of years until anatomically modern *H. sapiens* from Africa invaded their turf. Then the Neandertals faded away. Some experts have proposed that Neandertals lost out to the moderns because they lacked the language and social skills, technological ingenuity and foraging savvy that the newcomers had. Any hints of Neandertal sophistication from late Neandertal archaeological sites were chalked up to the influence of *H. sapiens.* Recent efforts to pinpoint the timing of Neandertal extinction, by redating a number of sites in Europe, indicate that Neandertals overlapped with *H. sapiens* for thousands of years in some places—ample time for Neandertals to have learned the ways of the interlopers. Yet over the past several years a flurry of discoveries attesting to Neandertal sophistication—from symbolic items and advanced tools to a wide variety of food remnants—have emerged from sites that clearly predate the arrival of *H. sapiens.* The question that scientists now face is whether the new arrivals were just better at these things or whether some other factor drove the Neandertals' demise.

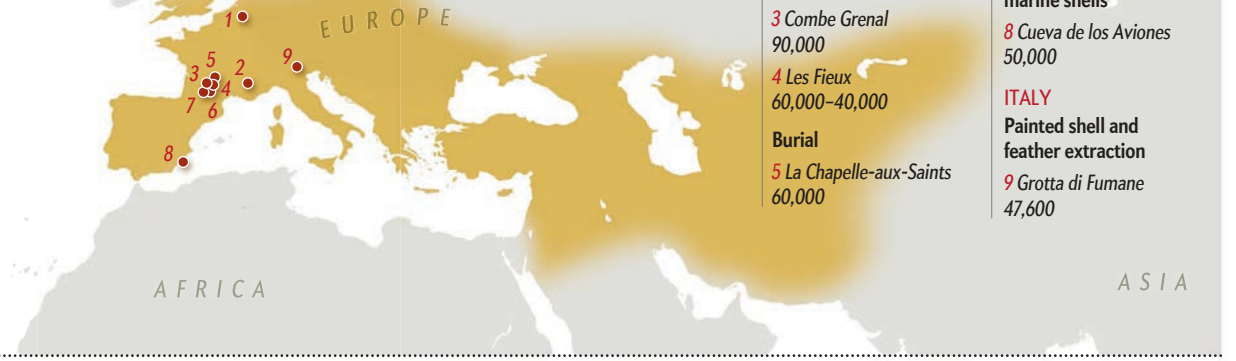
Neandertal range

Early *Homo sapiens* range

Representative sites of Neandertal finds indicative of advanced behavior

250,000–45,000 Years Ago

The Neandertal range reached its greatest extent in this time frame. A number of Neandertal sites show signs of sophisticated behavior that may predate the arrival of anatomically modern humans.



THE NETHERLANDS

Liquid pigment

1 Maastricht-Belvedere 250,000–200,000 years ago

FRANCE

String, array of plant and animal remains, and possible projectile weapons

2 Abri du Maras 90,000

Eagle talons

3 Combe Grenal 90,000

4 Les Fieux 60,000–40,000

Burial

5 La Chapelle-aux-Saints 60,000

Leather-burnishing tools

6 Pech-de-l'Azé 53,400–49,400

7 Abri Peyrony 47,700–41,000

SPAIN

Pigment-stained marine shells

8 Cueva de los Aviones 50,000

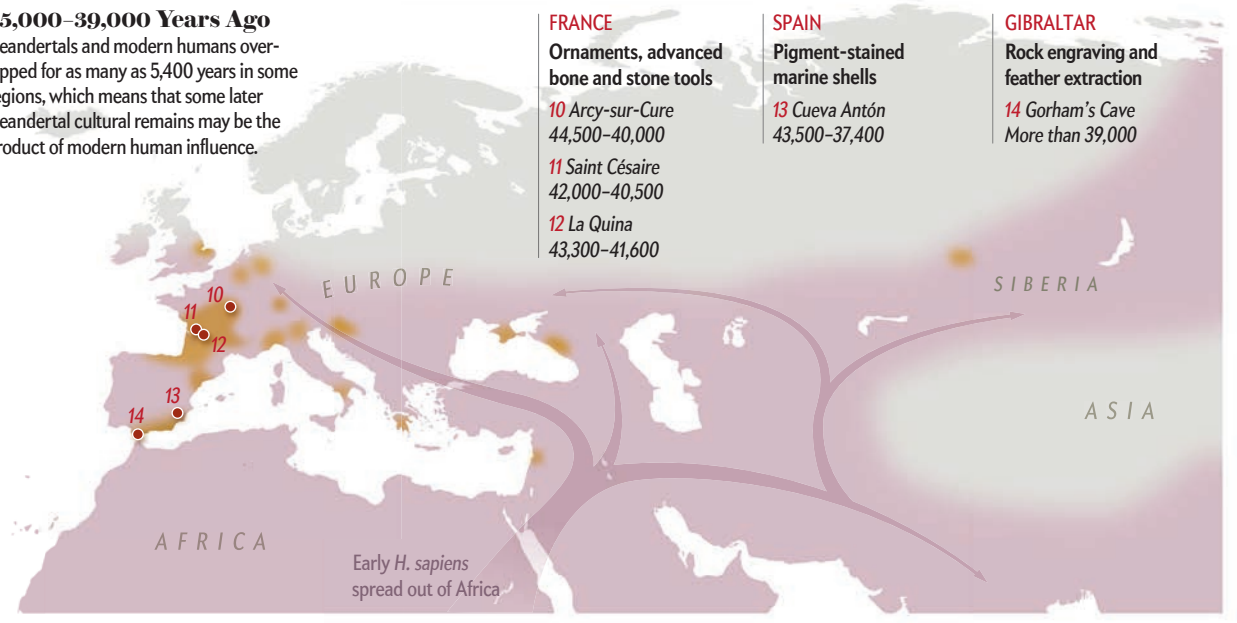
ITALY

Painted shell and feather extraction

9 Grotta di Fumane 47,600

45,000–39,000 Years Ago

Neandertals and modern humans overlapped for as many as 5,400 years in some regions, which means that some later Neandertal cultural remains may be the product of modern human influence.



FRANCE

Ornaments, advanced bone and stone tools

10 Arcy-sur-Cure 44,500–40,000

11 Saint Césaire 42,000–40,500

12 La Quina 43,300–41,600

SPAIN

Pigment-stained marine shells

13 Cueva Antón 43,500–37,400

GIBRALTAR

Rock engraving and feather extraction

14 Gorham's Cave More than 39,000

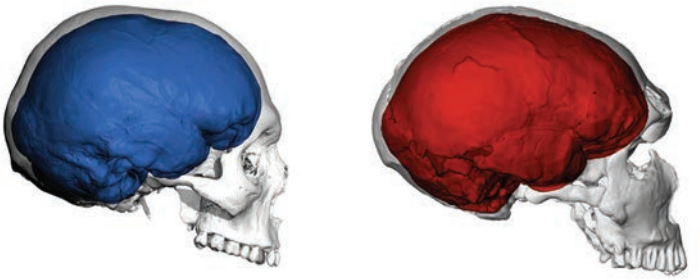
SOURCE: "THE TIMING AND SPATIOTEMPORAL PATTERNING OF NEANDERTHAL DISAPPEARANCE," BY TOM HIGHAM ET AL., IN *NATURE*, VOL. 512, AUGUST 21, 2014 (*Neandertal range*)

THE STORY OF US

Map by 5W Infographics

Blangero realized that with the aid of their statistical tool, they could use the Neandertal genomes and his group's genetic and MRI data from living people to estimate the effects of the full complement of Neandertal genetic variants—the so-called polygenotype—on traits related to cognition.

Their results suggest that several key brain regions were smaller in Neandertals than in modern humans, including the gray matter surface area (which helps to process information in the brain), Broca's area (which seems to be involved in language) and the amygdala (which controls emotions and motivation). The findings also indicate that Neandertals would have had less white matter, translating to reduced brain connectivity. And other traits would have compromised their ability to learn and remember words. "Neandertals were almost certainly less cognitively adept," asserts Blangero, who presented his preliminary findings at the annual meeting of the American Association of Physical Anthropologists in 2014. "I'm willing to bet on that one."



BRAIN SHAPE differs between a modern human (*blue*) and a Neandertal (*red*), but how this difference might have affected thought is unknown.

Of course, without living Neandertals around today, Blangero cannot conduct cognitive assessments that would confirm or refute his inference. But there is, in theory, another way to put his hunch to the test. It would be possible, using existing technology, to study Neandertal brain cell function by genetically modifying modern human cells to have Neandertal DNA sequences, programming them to become neurons and observing the Neandertalized cells in petri dishes. Scientists could then examine the abilities of the neurons to conduct electrical impulses, to migrate to different brain regions and to produce projections (neurites) that aid in cell communication, for instance. Blangero notes that although there are ethical issues to consider where the creation of Neandertal cells is concerned, such work might actually help researchers identify genes involved in modern human brain disorders if the genetic changes compromise neuron function. Such findings could, in turn, lead to the discovery of new drug targets.

Not everyone is ready to draw conclusions about the Neandertal mind from DNA. John Hawks of the University of Wisconsin–Madison observes that Neandertals may have carried gene variants that affected their brain function but that have no counterparts in people today for comparison. He notes that if one were to predict Neandertal skin color based on the genes they share with modern humans, one would surmise that they had dark skin. Yet scientists now know Neandertals had some genes no longer in circulation that probably lightened their skin. But a bigger problem with attempting to suss out how Neandertal brains worked from their genes, Hawks says, is that for the most part researchers do not know how genes affect thought in our own kind. "We know next to nothing about Neandertal cognition from genetics because we know next to nothing about [modern] human cognition from genetics," he asserts.

ARCHAEOLOGICAL INSIGHTS

GIVEN THE LIMITATIONS of the fossil anatomy and the fact that ancient DNA research is still in its infancy, many researchers say the clearest window on the Neandertal mind is the cultural record these extinct humans left behind. For a long time, that record did not paint a particularly flattering picture of our vanished cousins. Early modern Europeans left behind elegant art, complex tools and remainders of meals attesting to an ability to exploit a wide variety of animals and plants that enabled them to adapt to new environments and shifting climate. Neandertals, in contrast, seemed to lack art and other symbolic remains; their tools were comparatively simple; and they appeared to have had a foraging strategy narrowly focused on large game. Stuck in their ways, the thinking went, the Neandertals simply could not adapt to deteriorating climate conditions and competition from the invading moderns.

In the 1990s, however, archaeologists began to find evidence contradicting that scenario—namely, a handful of decorative items and advanced tools attributed to Neandertals. Ever since, researchers have been at loggerheads over whether these items are Neandertal inventions as claimed; doubt has arisen because the items date to the end of the Neandertal dynasty, by which time *H. sapiens* was in the area, too. (Anatomically modern humans appear to have reached Europe by around 44,000 to 41,500 years ago, hundreds of thousands of years after Neandertals settled there.) Some skeptics think that *H. sapiens* made the sophisticated artifacts, which later got mixed in with the Neandertal remains. Alternatively, they offer, Neandertals may have copied the ingenious moderns or stolen their goods.

But that position is becoming harder to uphold in the face of a raft of discoveries over the past few years that evince Neandertal savvy prior to the spread of anatomically modern humans throughout Europe. "There's been a real sea change. Every month brings something new and surprising that Neandertals did," observes David Frayer of the University of Kansas. "And the new evidence is always that they were more sophisticated, not hicks."

Some of the most surprising discoveries reveal aesthetics and abstract thought in Neandertal cultures that predated the arrival of *H. sapiens*. These finds include the engraving and signs of feather use from Gorham's Cave. In fact, artifacts of this nature have turned up at archaeological sites across Europe. At the Grotta di Fumane in Italy's Veneto region, archaeologists found signs of feather use and a fossil snail shell collected from at least 100 kilometers away that had been stained red, suspended on a string and worn as a pendant at least 47,600 years ago. Cueva de los Aviones and Cueva Antón in southeastern Spain have also yielded seashells bearing traces of pigment. Some seem to have served as cups for mixing and holding red, yellow and sparkly black pigments that may have been cosmetics; others bear holes indicating that they were worn as jewelry. The modified shells date to as many as 50,000 years ago.

Other Neandertal leavings indicate that their yen for decorat-

FROM "A UNIQUELY MODERN HUMAN PATTERN OF ENDOCRANIAL DEVELOPMENT: INSIGHTS FROM A NEW CRANIAL RECONSTRUCTION OF THE NEANDERTAL NEWBORN FROM MEZMAISKAYA," BY PHILIPP GUNZ, SIMON NEUBAUER, LUBOV GOLOVANOVA, VLADIMIR DORONICHEV, BRUNO MAUREILLE AND JEAN-JACQUES HUBLIN, IN *JOURNAL OF HUMAN EVOLUTION*, VOL. 62, NO. 2; FEBRUARY 2012

GIBRALTAR CAVES (*1*) housed sophisticated Neandertals. An engraving (*2*) found in one of the caves adds to evidence that Neandertals thought symbolically.

ing reaches back further still. Sites in France and Italy document a tradition of harvesting eagle talons that spans from 90,000 to 40,000 years ago. Cut marks on the bones show that the Neandertals focused their efforts on obtaining the claws, not the flesh, suggesting that they exploited the eagles for ornamentation—probably to adorn themselves with the impressive talons—rather than food. In 2015 researchers reported another such find from the Croatian site of Krapina dating to 130,000 years ago.

Even older hints of Neandertal aesthetics come from the site of Maastricht-Belvedere in the Netherlands, where archaeologists have found small splatters of red ocher, or iron oxide, in deposits dating to between 250,000 and 200,000 years ago at minimum. The scarlet pigment had been finely ground and mixed into a liquid that then dripped onto the ground. No one can say for sure what those Neandertals were doing with the red liquid, but painting is one obvious possibility. In 2016 researchers announced their discovery of 176,000-year-old structures made from carefully arranged pieces of stalagmites in Bruniquel Cave in France. These structures might represent symbolic activity, but their exact purpose remains unknown.

In addition to rendering a far more resplendent portrait of our much maligned cousins, these new discoveries provide crucial insights into the Neandertal mind. Archaeologists have long considered art, including body decoration, to be a key indicator of modern cognitive abilities because it means that the makers had the capacity to conceive of something in the abstract and to convey that information in symbols. Symbolic thinking underpins our ability to communicate via language—one of the defining traits of modern humans and one that is seen as critical to our success as a species. If Neandertals thought symbolically, as they appear to have done, then they probably had language, too. In fact, abstract thought may have dawned in the human lineage even before the last common ancestor of Neandertals and *H. sapiens:* in 2014 researchers unveiled a mussel shell from Indonesia that they contend was engraved with a geometric pattern by a more primitive ancestor, *Homo erectus,* around 500,000 years ago.

Symbolic thought is not the only component of behavior believed to have helped *H. sapiens* get ahead, however. The manufacture of tools with specialized uses is another element, one that Neandertals appear to have mastered as well. In 2013 Marie Soressi of Leiden University in the Netherlands and her collaborators announced their discovery of bone tools known as *lissoirs*—implements that leather workers today use to render animal hides more pliable, lustrous and impermeable to the elements—at two Neandertal sites in the Dordogne region of France dating to between 53,000 and 41,000 years ago. Judging from the wear marks on the artifacts, Neandertals used them for the same purpose. The Neandertals made the *lissoirs* from deer ribs, shaping the end of the bone that attaches to the sternum to form a rounded tip that they would push across a dry hide to smooth and soften the skin.

Evidence of Neandertal ingenuity has also come from the site of Abri du Maras in southern France, which sheltered Neandertals around 90,000 years ago. Microscopic analyses of stone tools from the site, conducted by Bruce Hardy of Kenyon College and his colleagues, revealed traces of all manner of activities once thought to be beyond the ken of the species. For instance, the team found remnants of twisted plant fibers that would have been used for making string or cords, which then could have been fashioned into nets, traps and bags. Traces of wood turned up as well, suggesting that the Neandertals crafted tools from that material.

Residue analysis additionally gives the lie to the notion that Neandertals were perilously picky eaters. Studies of the chemical makeup of their teeth, along with analyses of animal remains

DAVID LIITTSCHWAGER *National Geographic Creative* (*1*); COURTESY OF STEWART FINLAYSON *The Gibraltar Museum* (*2*)

BONE TOOL for leatherwork, shown here in four views, is among the advanced implements that Neandertals made.

COURTESY OF SHANNON P. MCPHERRON, © ABRI PEYRONY PROJECT

from Neandertal sites, have suggested that Neandertals relied heavily on large, dangerous prey such as mammoth and bison rather than an array of animals depending on availability, as anatomically modern humans did. The Abri du Maras Neandertals exploited a menagerie of creatures, including small, fast animals such as rabbits and fish—species previously thought to be out of reach for Neandertals, with their low-tech gear.

Some scholars have argued that an ability to live partly on plant foods gave *H. sapiens* an edge over Neandertals, allowing them to reap more sustenance from the same area of land. (Subsisting on plants is trickier for humans than for other primates because our big brains demand a lot of calories, and yet our small guts are poorly suited to digesting large quantities of raw roughage—a combination that requires intimate knowledge of plant foods and how to prepare them.) But the Abri du Maras Neandertals gathered edible plants, including parsnip and burdock, as well as edible mushrooms. And they were not alone.

According to studies led by Amanda Henry of the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, Neandertals across a broad swath of Eurasia—from Iraq to Belgium—ate a variety of plants. Examining the tartar in Neandertal teeth and residues on stone tools, she determined that Neandertals consumed species closely related to modern wheat and barley, cooking them to make them palatable. She also found bits of starch from tubers and telltale components of date palms. The similarities to findings from early modern human sites were striking. "Any way we broke up the data, there were no significant differences between the groups," Henry remarks. "The evidence we have now does not suggest that the earliest modern humans in Eurasia were better at accessing plant foods."

A LONG FAREWELL

IF NEANDERTALS actually behaved in ways once thought to distinguish anatomically modern humans and fuel their rise to world domination, that likeness makes their decline and eventual extinction all the more puzzling. Why did they die out while *H. sapiens* survived? One theory is that moderns had a bigger tool kit that may have boosted their foraging returns. Modern humans evolved in Africa, where their population size was larger than that of Neandertals, Henry explains. With more mouths to feed, preferred resources such as easy game would have declined, and the moderns would have had to develop new tools to obtain other kinds of food. When they brought this cutting-edge technology with them out of Africa and into Eurasia, they were able to exploit that environment more effectively than the resident Neandertals could. In other words, moderns honed their survival skills under more competitive circumstances than Neandertals had faced and thus entered Neandertal territory with an advantage over the incumbents.

Not only did the large population size of *H. sapiens* spur innovation, but it helped to keep new traditions alive rather than letting them fizzle out with the last member of a small, isolated group. The bigger, more connected membership of *H. sapiens* "increasingly provided a more efficient ratchet effect to maintain and build on knowledge compared with earlier humans, including the Neandertals," offers Christopher Stringer of the Natural History Museum in London. Still, the arrival of moderns did not spell instant doom for Neandertals. An attempt to track their decline, carried out by Thomas Higham of Oxford and his colleagues in 2014, applied improved dating methods to pinpoint the ages of dozens of Neandertal and early modern European sites from Spain to Russia. The results indicate that the two groups shared the continent for some 2,600 to 5,400 years before the Neandertals finally disappeared, around 39,000 years ago.

That lengthy overlap would have left plenty of time for mating between the two factions. DNA analyses have found that people today who live outside Africa carry an average of least 1.5 to 2.1 percent Neandertal DNA—a legacy from dalliances between Neandertals and anatomically modern humans tens of thousands of years ago, after the latter group began spreading out of Africa.

Maybe, some experts offer, mixing between the smaller Neandertal population and the larger modern one led to the Neandertals' eventual demise by swamping their gene pool. "There were never very many of them, there were people coming in from other areas and mixing with them, and they faded out," Kansas's Frayer surmises. "The history of all living forms is that they go extinct," he adds. "That's not necessarily a sign that they were stupid, or culturally incapable, or adaptively incapable. It's just what happens." SA

Kate Wong is a senior editor at *Scientific American*.

MORE TO EXPLORE

Brain Development after Birth Differs between Neanderthals and Modern Humans. Phillip Gunz et al. in *Current Biology*, Vol. 20, No. 21, pages R921–R922; November 9, 2010.

Impossible Neanderthals? Making String, Throwing Projectiles and Catching Small Game during Marine Isotope Stage 4 (Abri du Maras, France). Bruce L. Hardy et al. in *Quaternary Science Reviews*, Vol. 82, pages 23–40; December 15, 2013.

A Rock Engraving Made by Neanderthals in Gibraltar. Joaquín Rodríguez-Vidal et al. in *Proceedings of the National Academy of the Sciences USA*, Vol. 111, No. 37, pages 13,301–13,306; September 16, 2014.

scientificamerican.com/magazine/sa

Bonding
Kinship

Powers of Two

Pairing up might have been the best move our ancestors ever made

By Blake Edgar

IN BRIEF

Even in societies where polygamy is permitted, monogamy is by far the most common human mating arrangement. In this regard, we are unusual animals: fewer than 10 percent of mammals form exclusive sexual relationships.

How humans got to be this way has been the subject of scientific debate for decades, and it is still an open question. New research, however, is helping to clarify matters.

We now know that the first hominins, which emerged more than seven million years ago, might have been monogamous. Humans stayed (mostly) monogamous for good reason: it helped them evolve into the big-brained world conquerors they are today.

Illustration by Martin O'Neill

MAMMALS ARE NOT BIG ON MONOGAMY. IN FEWER THAN 10 PERCENT OF species is it common for two individuals to mate exclusively. The primate wing of the group is only slightly more prone to pairing off. Although 15 to 29 percent of primate species favor living together as couples, far fewer commit to monogamy as humans know it—an exclusive sexual partnership between two individuals.

When it comes to monogamy, humans obviously have an imperfect track record. People have affairs, get divorced and, in some cultures, marry multiple mates. In fact, polygamy appears in most of the world's societies. Yet even where polygamy is permitted, it is the minority arrangement. Most human societies are organized around the assumption that a large fraction of the population will pair off into enduring, sexually exclusive couples. And monogamy seems to have done our species good. "Pair bonds," as scientists call monogamous relationships, were a crucial adaptation that arose in an archaic forebear and became central to human social systems and our evolutionary success. "We have a very big advantage over many other species by having pair bonds," says University of Montreal anthropologist Bernard Chapais.

The monogamous couple also forms the basis for something uniquely human—the vast, complex social networks in which we live. Other primate young establish kinship links only through their mother; humans trace kinship from both parents, broadening each generation's family ties. Among humans, social networks extend to include other families and even unrelated groups in widening ripples of relationships. In Chapais's view, such group ties, along with monogamy, constitute "two of the most consequential features of human society."

Scientists have struggled for decades to understand the origins and implications of human monogamy. Basic questions such as when we started to pair up for life, why it was advantageous and how coupling might have spurred our success as a species remain unresolved and contentious, but new research has brought us closer to solving the mystery.

THE ORIGINS OF COUPLING

IT IS ENTIRELY POSSIBLE that our most distant ancestors were monogamous. Fossil evidence, says anthropologist C. Owen Lovejoy of Kent State University, suggests that monogamy predates even *Ardipithecus ramidus,* the species best known from a 4.4-million-year-old partial female skeleton, nicknamed "Ardi," discovered in the Middle Awash region of Ethiopia. In Lovejoy's hypothesis, soon after the split from the last common ancestor between the great ape and human evolutionary branches more than seven million years ago, our predecessors adopted a transformative trio of behaviors: carrying food in arms freed by bipedal posture, forming pair bonds and concealing external signals of female ovulation. Evolving together, these innovations gave hominins, the tribe that emerged when early humans diverged from chimpanzees, a reproductive edge over apes.

According to this hypothesis, an ancestral polygamous mating system was replaced by pair bonding when lower-ranked hominin males diverted energy from fighting one another toward finding food to bring to females as an incentive to mate. Females preferred reliable providers to aggressive competitors and bonded with the better foragers. Eventually females lost the skin swelling or other signs of sexual receptivity that would have attracted different males while their partners were off gathering food.

For evidence, Lovejoy points to *Ar. ramidus*'s teeth. Compared with living and fossil apes, *Ar. ramidus* shows a stark reduction in the differences between male and female canine-tooth size. Evolution has honed the daggerlike canines of many

THOMAS MARENT AGE Fotostock

SILVERBACK MALE mountain gorilla and his troop in the forest. Mountain gorillas, which are polygamous, live in small groups that usually consist of one dominant male, multiple female mates and their offspring.

male primates into formidable weapons used to fight for access to mates. Not so for early hominins. Picture the canines in a male gorilla's gaping jaws; now peer inside your own mouth. Humans of both sexes have small, stubby canines—an unthreatening trait unique to hominins, including the earliest *Ardipithecus* specimens.

A rough correlation also exists between mating behavior in primates and sexual dimorphism—that is, differences in body mass and size between males and females of the same species. The more dimorphic a primate species is, the more likely it is that males fight over females. At one extreme, polygamous gorilla males grow to be more than twice as massive as females. At the opposite extreme, both male and female gibbons, which are mainly monogamous, are nearly equal in mass. Humans lie closer to gibbons on the dimorphism spectrum: human males can be up to 20 percent more massive, on average, than females.

There is only so much we can make of the fossil record, though. Paleoanthropologist J. Michael Plavcan of the University of Arkansas urges caution in making the leap from fossilized bones to social behavior in hominins. Consider *Australopithecus afarensis,* the species to which "Lucy" belonged, which lived between 3.9 million and three million years ago. Like *Ardipithecus, A. afarensis* had small canines, but its skeleton displays a level of dimorphism between that of modern chimpanzees and gorillas. "You have [a level of] body-size dimorphism suggesting that [*A. afarensis*] males were competing for females and [a] loss of canine dimorphism that suggests they weren't," Plavcan says. "It's a puzzle."

Many anthropologists also dispute Lovejoy's conclusion that monogamy nurtured by males providing food for their mates and offspring has been a hominin strategy for millions of years. In April 2013 in the journal *Evolutionary Anthropology,* Chapais argued that the unique features of human family and social structure (monogamy, kinship ties through both parents and expanding social circles) emerged in a stepwise sequence. Before the first step, Chapais said, both male and female hominins were, like chimpanzees, promiscuous with partners. Then came a transition to polygamy, which is found in gorillas. But keeping many mates is hard work. It involves a lot of fighting with other males and guarding females. Monogamy might have emerged as the best way to reduce the effort of polygamy.

Chapais declines to speculate about when this shift happened and what species were involved. But other researchers

are homing in on the period between two million and 1.5 million years ago, after the origin of our genus *Homo* and coincident with physical changes that show up in *Homo erectus,* most likely the first hominin species to successfully migrate beyond Africa. *H. erectus* possessed a much larger body, proportioned more like that of a modern human, than its predecessors. Roughly twice the size of Lucy's species, *H. erectus* also seems to be less sexually dimorphic than australopithecines and the earliest members of *Homo*. Limited fossil evidence suggests that *H. erectus* females started to approach the physical stature of males and to have a similar degree of dimorphism as in modern humans, which together could suggest that *H. erectus* had a less competitive way of life than its ancestors. Because primates with similar body sizes tend to be monogamous, this change could signal a shift toward more exclusive mating behavior. *Homo naledi*, an extinct hominin reported in 2015 but not yet dated, seems to follow a similar body-size trend. Some 1,550 fossils from at least 15 individuals show remarkably little size variation among the same bones in different adult skeletons.

A STRATEGIC PARTNERSHIP

IF SCIENTISTS CANNOT AGREE on when humans became monogamous, we can hardly expect them to agree on why it happened. In 2013 two independent research teams published separate statistical studies of existing literature to determine which behaviors could have been drivers of monogamy. Both studies aimed to find the best explanation for monogamy among three persistent hypotheses: female spacing, infanticide avoidance and male parental care.

The female-spacing hypothesis posits that monogamy arises after females begin to establish larger territories to gain more access to limited food resources and, in the process, put more distance between one another. With females farther apart, males have a harder time finding and keeping multiple mates. Settling down with a single partner makes life easier, reducing a male's risk of being injured while patrolling his territory and enabling him to ensure that his mate's offspring are his own.

Zoologists Dieter Lukas and Tim Clutton-Brock, both at the University of Cambridge, found evidence for this idea in a statistical analysis of 2,545 species of mammals. They described their findings in a paper published in *Science*. The data indicated to them that mammals started out solitary, but then one species or another switched to monogamy 61 different times during their evolutionary history. Monogamy most frequently emerged in carnivores and primates, suggesting that species will tend toward mating in pairs when its females require a rich but rare diet (such as protein-rich carcasses or ripe fruits) that can usually be obtained only by searching a large area. Their findings provided the strongest statistical support for the conclusion that increasingly scattered, solitary females drove males to solicit single partners.

Lukas acknowledges that although the hypothesis may work for nonhumans, it might not be so apt for humans: it is difficult to reconcile the inherent sociality of humans with a hypothesis that depends on a low density of available females. It may be that our ancestors were too social for females to have been scattered across the savanna like other mammals. But the theory could potentially hold for humans if monogamy arose in hominins before our tendency to dwell in groups did.

AZARA'S OWL MONKEYS of South America are fully monogamous, with the father handling much of the child care.

ART WOLFE *Getty Images*

The second leading hypothesis holds that monogamy originated from the threat of lethal violence toward offspring. If a rival male challenged or supplanted a dominant male in a community, the usurper could kill infants that he had not sired. Mothers would stop lactating and start ovulating again, giving the marauding male a chance to spread his genes. To prevent infanticide, a female would select a male ally who could defend her and her baby.

Anthropologist Kit Opie of University College London cites evidence for the infanticide-avoidance hypothesis in a study published in the *Proceedings of the National Academy of Sciences*. Opie and his colleagues ran computer simulations of primate evolutionary history for 230 primate species; they then applied what is called a Bayesian statistical analysis to determine which of the three prominent hypotheses for the origin of monogamy had the highest probability of being correct. They identified a significant correlation between monogamy in primates and each of the three hypothetical triggers, but only an increase in the threat of infanticide consistently preceded the appearance of monogamy in multiple primate lineages.

The biology and behavior of modern primates add some plausibility to the conclusion that infanticide is a spur to monogamy. Primates are uniquely at risk for infanticide: they have big brains that need time to develop, which leaves babies dependent and vulnerable for long periods after birth. And the killing of babies has been observed in more than 50 primate species; it typically involves a male from outside a group attacking an unweaned infant in a bid for dominance or access to

females. But there are limits to the evidence: nearly all these species have either promiscuous or polygamous mating systems, so the distribution of infanticide in living primates does not fit the prediction that monogamy should evolve when infanticide is a big threat.

The third hypothesis for why monogamy evolved involves a male contributing to parental duties. When a baby becomes too costly in terms of calories and energy for a mother to raise on her own, the father who stays with the family and provides food or other forms of care increases his offspring's chances of survival and thereby encourages closer ties with the mother.

A related idea, proposed by anthropologist Lee Gettler of the University of Notre Dame, holds that the mere carrying of offspring by fathers fosters monogamy. Mothers have to meet the considerable nutritional demands of nursing infants. Yet for primates and human hunter-gatherers, hauling an infant, especially without the benefit of a sling or other restraint, required an expense of energy comparable to breast-feeding. Carrying by males could have freed females to fulfill their own energetic needs by foraging.

KEEPING MANY MATES IS HARD WORK. IT INVOLVES A LOT OF FIGHTING WITH OTHER MALES AND GUARDING FEMALES. MONOGAMY MIGHT HAVE EMERGED AS A WAY TO REDUCE THAT EFFORT.

South America's Azara's owl monkey may offer some insight into how paternal care would reinforce monogamy. These monkeys live in small family groups, with an adult male-and-female pair and an infant, plus a juvenile or two. A mother monkey carries a newborn on her thigh just after birth. But the baby's father assumes most of the carrying and caretaking—grooming, playing and feeding—from the time the baby is two weeks old. The adult partners literally stay in touch with frequent tail contact, and the male's mere proximity to both the female and his young may strengthen emotional ties.

Indeed, a study published in March 2014 in the *Proceedings of the Royal Society B* presented genetic evidence that Azara's owl monkey pairs remain monogamous—the first genetic confirmation for any nonhuman primate. DNA collected from several study groups revealed that all the females and all but one of the males in 17 pairs were the most likely parents of 35 offspring. "They go all the way and commit to a monogamous relationship in genetic terms," says anthropologist Eduardo Fernandez-Duque of Yale University, a co-author of the study. Mating bonds between Azara's owl monkeys last an average of nine years, and monkeys that stay with the same partner achieve greater reproductive success—the end game of evolution under any mating system.

What do the two recent statistical studies have to say about the paternal care hypothesis? Both concluded that paternal care seemed the least likely among the competing hypotheses to trigger monogamous mating—but, Lukas says, "paternal care may still explain why a species *stays* monogamous."

IT TAKES A VILLAGE

A MONOGAMOUS SET of parents is not enough to raise an ape as smart and social as a human, says anthropologist Sarah Hrdy of the University of California, Davis. A human baby consumes some 13 million calories on its long journey from birth to maturity, a heavy burden for a mother to bear even with a mate helping. This demand might explain why in many societies, human mothers rely on "alloparents" (such as the kin of either parent or other group members) to help provide food and child care. "Human mothers are willing to let others hold their babies right from birth," Hrdy observes. "That's amazing, and it's remarkably unapelike." No ape engages in anything like alloparenting.

Hrdy maintains that cooperative breeding, a social system in which alloparents help care for young, evolved among our ancient ancestors starting with *H. erectus* nearly two million years ago. This species had a much larger body and brain than its ancestors; by one estimate, it took 40 percent more metabolic energy to run an *H. erectus* body relative to previous hominins. If *H. erectus* started down a humanlike path of delayed development and prolonged dependency, cooperative alloparents might have been required to support the energetic demands of raising bigger-brained babies.

Without cooperative breeding, conclude Karin Isler and Carel van Schaik, both at the University of Zurich, early *Homo* would not have broken through the hypothetical "gray ceiling" that constrains an ape's brain to a maximum volume of about 700 cubic centimeters. To pay the energetic cost of having an enlarged brain, an animal must reduce its rate of birth or its rate of growth, or both. But humans have achieved shorter weaning periods and greater reproductive success than a creature with a brain volume ranging from 1,100 to 1,700 cubic centimeters should have been able to. Isler and van Schaik attribute this success to alloparenting, which enabled *H. erectus* to have offspring more frequently while providing those offspring enough energy to grow a large brain.

It was cooperation, then, whether in the form of monogamous pairs, nuclear families or tribes, that enabled humans to succeed when all our fossil ancestors and cousins went extinct. In fact, cooperation may be the greatest skill we have acquired during the past two million years—one that enabled our young genus to survive through periods of environmental change and stress. And one that may well determine our geologically young species' future. SA

Blake Edgar is co-author of *From Lucy to Language* (revised and expanded edition, Simon & Schuster, 2006) and other books and is a contributing editor at *Archaeology Magazine*.

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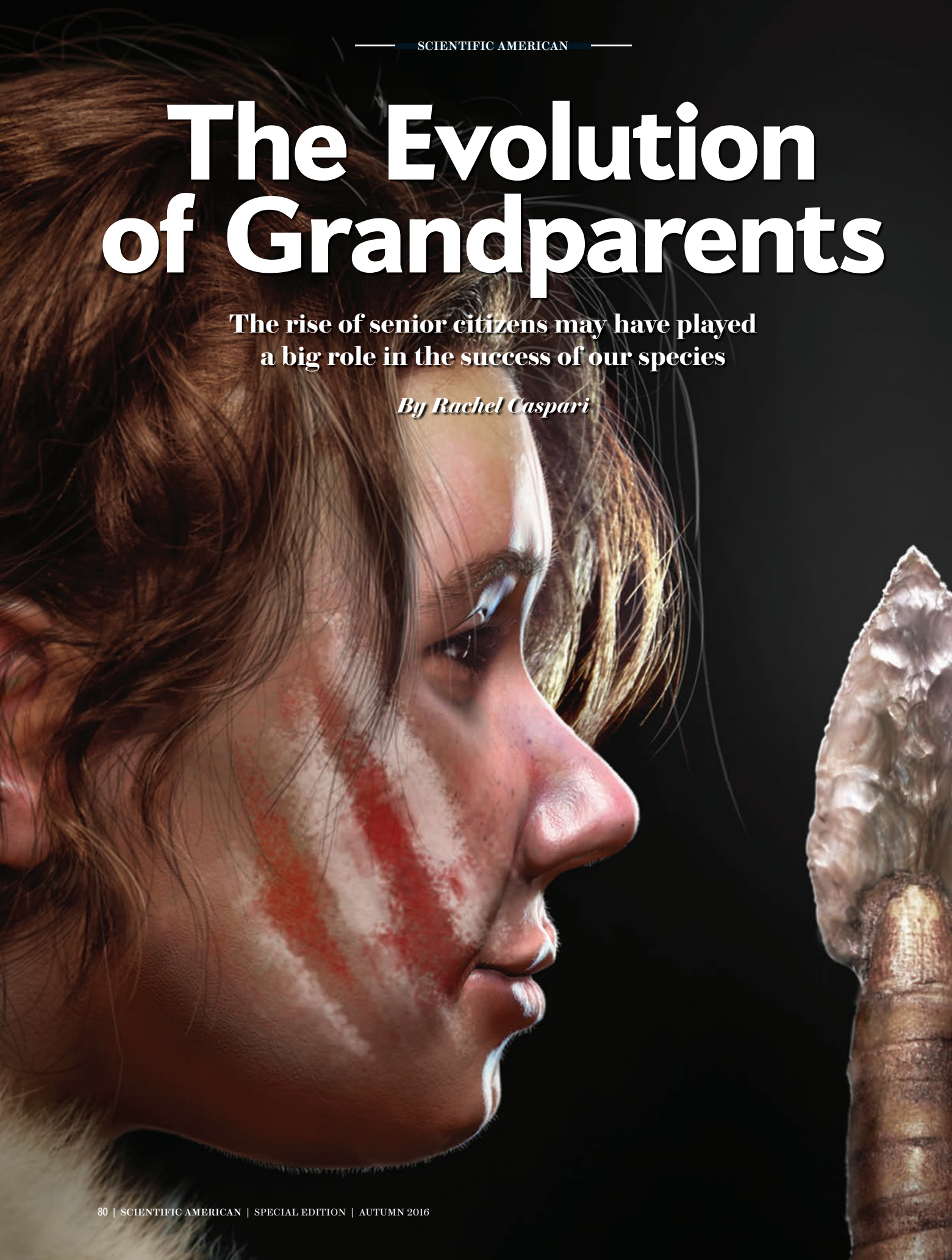
The Evolution of Grandparents

The rise of senior citizens may have played a big role in the success of our species

By Rachel Caspari



IN BRIEF

People today typically live long enough to become grandparents, but this was not always the case.
Recent analyses of fossil teeth indicate that grandparents were rare in ancient populations, such as those of the australopithecines and the Neandertals. They first became common around 30,000 years ago, as evidenced by remains of early modern Europeans.
This surge in the number of seniors may have been a driving force for the explosion of new tool types and art forms that occurred in Europe at around the same time. It may also explain how modern humans outcompeted archaic groups such as the Neandertals.

Illustration by Viktor Deak

DURING THE SUMMER OF 1963, WHEN I WAS SIX YEARS OLD, MY FAMILY traveled from our home in Philadelphia to Los Angeles to visit my maternal relatives. I already knew my grandmother well: she helped my mother care for my twin brothers, who were only 18 months my junior, and me. When she was not with us, my grandmother lived with her mother, whom I met that summer for the first time. I come from a long-lived family. My grandmother was born in 1895 and her mother in the 1860s; both lived almost 100 years. We stayed with the two matriarchs for several weeks. Through their stories, I learned about my roots and where I belonged in a social network spanning four generations. Their reminiscences personally connected me to life at the end of the Civil War and the Reconstruction era and to the challenges my ancestors faced and the ways they persevered.

My story is not unique. Elders play critical roles in human societies around the globe, conveying wisdom and providing social and economic support for the families of their children and larger kin groups. In our modern era, people routinely live long enough to become grandparents. But this was not always the case. When did grandparents become prevalent, and how did their ubiquity affect human evolution?

Research my colleagues and I have been conducting indicates that grandparent-aged individuals became common relatively recently in human prehistory and that this change came at about the same time as cultural shifts toward distinctly modern behaviors—including a dependence on sophisticated symbol-based communication of the kind that underpins art and language. These findings suggest that living to an older age had profound effects on the population sizes, social interactions and genetics of early modern human groups and may explain why they were more successful than archaic humans, such as the Neandertals.

LIVE FAST, DIE YOUNG

THE FIRST STEP in figuring out when grandparents became a fixture in society is assessing the typical age breakdown of past populations—what percent were children, adults of childbearing age and parents of those younger adults. Reconstructing the demography of ancient populations is tricky business, however. For one thing, whole populations are never preserved in the fossil record. Rather paleontologists tend to recover fragments of individuals. For another, early humans did not necessarily mature at the same rate as modern humans. In fact, maturation rates differ even among contemporary human populations. But a handful of sites have yielded high enough numbers of human fossils in the same layers of sediment that scientists can confidently assess the age at death of the remains—which is key to understanding the makeup of a prehistoric group.

A rock-shelter located in the town of Krapina in Croatia, about 40 kilometers northwest of the city of Zagreb, is one such site. More than a century ago Croatian paleontologist Dragutin Gorjanović-Kramberger excavated and described the fragmentary remains of perhaps as many as 70 Neandertal individuals there, most of which came from a layer dated to about 130,000 years ago. The large number of fossils found close to one another, the apparently rapid accumulation of the sediments at the site and the fact that some of the remains share distinctive, genetically determined features all indicate that the Krapina bones approximate the remains of a single population of Neandertals. As often happens in the fossil record, the best-preserved remains at Krapina are teeth because the high mineral content of teeth protects them from degradation. Fortunately, teeth are also one of the best skeletal elements for determining age at death, which is achieved by analyzing surface wear and age-related changes in their internal structure.

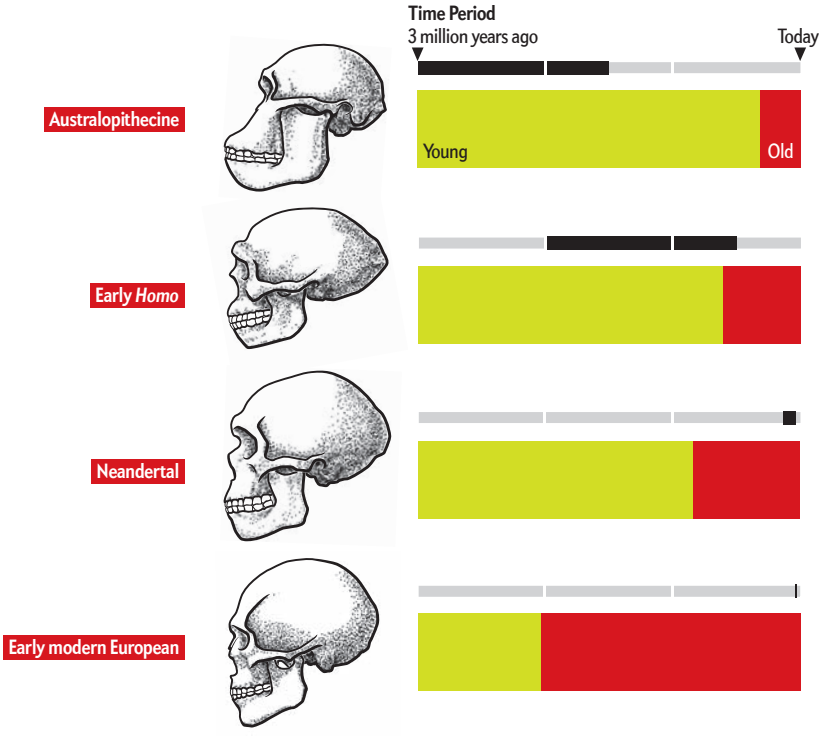
In 1979, before I began my research into the evolution of grandparents, Milford H. Wolpoff of the University of Michigan published a paper, based on dental remains, that assessed how old the Krapina Neandertals were when they died. Molar teeth erupt sequentially. Using one of the fastest eruption schedules observed in modern-day humans as a guide, Wolpoff estimated that the first, second and third molars of Neandertals erupted at ages that rounded to six, 12 and 15, respectively. Wear from chewing accumulates at a steady pace over a lifetime, so when the second molar emerges, the first already has six years of wear on it, and when the third emerges, the second has three years of wear.

Working backward, one can infer, for instance, that a first molar with 15 years of wear on it belonged to a 21-year-old Neandertal, a second molar with 15 years of wear on it belonged to a 27-year-old and a third molar with 15 years of wear on it belonged to a 30-year-old. (These estimates have an uncertainty of plus or minus one year.) This wear-based seriation method for determining age at death, adapted from a technique developed by dental researcher Albert E. W. Miles in 1963, works best on samples with large numbers of juveniles, which Krapina has in abun-

FINDINGS

Growing Older

Analyses of the fossilized teeth of hundreds of individuals spanning three million years indicate that living long enough to reach grandparenthood became common relatively late in human evolution. The author and her colleague assessed the proportion of older (grandparent-aged) adults relative to younger adults in four groups of human ancestors—australopithecines, early members of the genus *Homo*, Neandertals and early modern Europeans—and found that the ratio increased only modestly over the course of human evolution until around 30,000 years ago, when it skyrocketed.



dance. The method loses accuracy when applied to the teeth of elderly individuals, whose tooth crowns can be too worn to evaluate reliably and in some cases may even be totally eroded.

Wolpoff's work indicated that the Krapina Neandertals died young. In 2005, a few years after I began researching the evolution of longevity, I decided to take another look at this sample using a novel approach. I wanted to make sure that we were not missing older individuals as a result of the inherent limitations of wear-based seriation. With Jakov Radovčić of the Croatian Natural History Museum in Zagreb, Steven A. Goldstein, Jeffrey A. Meganck and Dana L. Begun, then all at Michigan, and undergraduate students from Central Michigan University, I worked to develop a new nondestructive method—using high-resolution three-dimensional microcomputed tomography (μCT)—to reassess how old the Krapina individuals were when they died. Specifically, we looked at the degree of development of a type of tissue within the tooth called secondary dentin; the volume of secondary dentin increases with age and provides a way to assess how old an individual was at death when the tooth crown is too worn to be a good indicator.

Our initial findings, supplemented with scans provided by the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, corroborated Wolpoff's results and validated the wear-based seriation method: the Krapina Neandertals had remarkably high mortality rates; no one there survived past age 30. (This is not to say that Neandertals never lived beyond 30. A few individuals from other sites were around 40 when they died.)

By today's standards, the Krapina death pattern is unimaginable. After all, for most people age 30 is the prime of life. And hunter-gatherers lived beyond 30 in the recent past. Yet the Krapina Neandertals are not unique among early humans. The few other human fossil localities with large numbers of individuals preserved, such as the approximately 600,000-year-old Sima de los Huesos site in Atapuerca, Spain, show similar patterns. The Sima de los Huesos people had very high levels of juvenile and young adult mortality, with no one surviving past 35 and very few living even that long. It is possible that catastrophic events or the particular conditions under which the remains became fossilized somehow selected against the preservation of older individuals at these sites. But the broad surveys of the human fossil record that my colleagues and I have conducted indicate that dying young was the rule, not the exception. To paraphrase words attributed to British philosopher Thomas Hobbes, prehistoric life really was nasty, brutish and short.

RISE OF THE GRANDPARENTS

THIS NEW μCT APPROACH has the potential to provide a high-resolution picture of the ages of older individuals in other fossil human populations. About a decade ago, before we hit on this technique, Sang-Hee Lee of the University of California, Riverside, and I were ready to start looking for evidence of changes in longevity over the course of human evolution. We turned to the best approach available at the time: wear-based seriation.

We faced a daunting challenge, though. Most human fossils do not come from sites, such as Krapina, that preserve so many individuals that the remains can be considered reflective of their larger populations. And the smaller the number of contemporaneous individuals found at a site, the more difficult it is to reliably estimate how old members were when they died because of the statistical uncertainties associated with small samples.

But we realized that we could get at the question of when grandparents started becoming common in another way. Instead of asking how long individuals lived, we asked how many of them lived to be old. That is, rather than focusing on absolute

SOURCE: "OLDER AGE BECOMES COMMON LATE IN HUMAN EVOLUTION," BY RACHEL CASPARI AND SANG-HEE LEE, IN *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES USA*, VOL. 101, NO. 30, JULY 27, 2004

Illustrations by Portia Sloan Rollings (skulls) and Jen Christiansen (graphic)

CONSEQUENCES

Culture Comes of Age

A marked increase in adult survivorship starting around 30,000 years ago in Europe may account for the dramatic cultural shift that ensued there as the comparatively simple technology of the Middle Paleolithic gave way to the sophisticated weapons and art of the Upper Paleolithic. Representative artifacts from both cultural traditions are shown here.

Middle Paleolithic
Flint point (*left*) and side scraper (*above*) from Le Moustier, France
Ceramic Venus figurine from Dolni Vestonice, Czech Republic
Upper Paleolithic
Bone flute from Hohle Fels, Germany
Stone burin from Brassempouy, France
ARTIFACTS NOT TO SCALE

ages, we calculated relative ages and asked what proportion of adults survived to the age at which one could first become a grandparent. Our objective was to evaluate changes over evolutionary time in the ratio of older to younger adults—the so-called OY ratio. Among primates, including humans up until very recently, the third molar erupts at about the same time that an individual becomes an adult and reaches reproductive age. Based on data from Neandertals and contemporary hunter-gatherer populations, we inferred that fossil humans got their third molars and had their first child at around age 15. And we considered double that age to mark the beginning of grandparenthood—just as some women today can potentially give birth at age 15 and those women can become grandmothers when their own children reach age 15 and reproduce.

For our purposes, then, any archaic individual judged to be 30 years old or more qualified as an older adult—one old enough to have become a grandparent. But the beauty of the OY ratio approach is that regardless of whether maturation occurred at 10, 15 or 20 years, the number of older and younger individuals in a sample would be unaffected because the start of older adulthood would change accordingly. And because we were only looking to place the fossils in these two broad categories, we could include large numbers of smaller fossil samples in our analysis without worrying about uncertainties in absolute ages.

We calculated the OY ratios for four large aggregates of fossil samples totaling 768 individuals spanning a period of three million years. One aggregate comprised later australopithecines, who lived in Africa from three million to 1.5 million years ago. Another aggregate consisted of early members of our genus, *Homo,* from around the globe who lived between two million and 500,000 years ago. The third group was the European Neandertals from 130,000 to 30,000 years ago. And the last consisted of modern Europeans from the early Upper Paleolithic period, who lived between about 30,000 and 20,000 years ago and left behind sophisticated cultural remains.

Although we expected to find increases in longevity over time, we were unprepared for how striking our results would turn out to be. We observed a small trend of increased longevity over time among all samples, but the difference between earlier humans and the modern humans of the Upper Paleolithic was a dramatic fivefold increase in the OY ratio. Thus, for every 10 young adult Neandertals who died between the ages of 15 and 30, there were only four older adults who survived past age 30; in contrast, for every 10 young adults in the European Upper Paleolithic death distribution, there were 20 potential grandparents. Wondering whether the higher numbers of burials at Upper Paleolithic sites might account for the high number of older adults in that sample, we reanalyzed our Upper Paleolithic sample, using only those remains that had not been buried. But we got similar results. The conclusion was inescapable: adult survivorship soared very late in human evolution.

BIOLOGY OR CULTURE?

NOW THAT LEE AND I had established that the number of potential grandparents surged at some point in the evolution of anatomically modern humans, we had another question on our

© THE NATURAL HISTORY MUSEUM, LONDON (*flint point and side scraper*); GETTY IMAGES (*Venus figurine and flute*); DIDIER DESCOUENS *Museum de Toulouse, France. https://commons.wikimedia.org/wiki/File:Burin_213_5_face.jpg* (*burin*)

hands: What was it that brought about this change? There were two possibilities. Either longevity was one of the many genetically controlled traits that biologically distinguished anatomically modern humans from their predecessors, or it did not come along with the emergence of modern anatomy and was instead the result of a later shift in behavior. Anatomically modern humans did not burst onto the evolutionary scene making the art and advanced weaponry that define Upper Paleolithic culture. They originated long before those Upper Paleolithic Europeans, more than 100,000 years ago, and for most of that time they and their anatomically archaic contemporaries the Neandertals used the same, simpler Middle Paleolithic technology. (Members of both groups appear to have dabbled in making art and sophisticated weapons before the Upper Paleolithic, but these traditions were ephemeral compared with the ubiquitous and enduring ones that characterize that later period.) Although our study indicated that a large increase in grandparents was unique to anatomically modern humans, it alone could not distinguish between the biological explanation and the cultural one, because the modern humans we looked at were both anatomically and behaviorally modern. Could we trace longevity back to earlier anatomically modern humans who were not yet behaviorally modern?

To address this question, Lee and I analyzed Middle Paleolithic humans from sites in western Asia dating to between about 110,000 and 40,000 years ago. Our sample included both Neandertals and modern humans, all associated with the same comparatively simple artifacts. This approach allowed us to compare the OY ratios of two biologically distinct groups (many scholars consider them to be separate species) who lived in the same region and had the same cultural complexity. We found that the Neandertals and modern humans from western Asia had statistically identical OY ratios, ruling out the possibility that a biological shift accounted for the increase in adult survivorship seen in Upper Paleolithic Europeans. Both western Asian groups had roughly even proportions of older and younger adults, putting their OY ratios between those of the Neandertals and early modern humans from Europe.

Compared with European Neandertals, a much larger proportion of western Asian Neandertals (and modern humans) lived to be grandparents. This is not unexpected—the more temperate environment of western Asia would have been far easier to survive in than the harsh ecological conditions of Ice Age Europe. Yet if the more temperate environment of western Asia accounts for the elevated adult survivorship seen in the Middle Paleolithic populations there, the longevity of Upper Paleolithic Europeans is even more impressive. Despite living in much harsher conditions, the Upper Paleolithic Europeans had an OY ratio more than double that of the Middle Paleolithic modern humans.

SENIOR MOMENTS

WE DO NOT KNOW EXACTLY what those Upper Paleolithic Europeans started doing culturally that allowed so many more of them to live to older age. But there can be no doubt that this increased adult survivorship itself had far-reaching effects. As Kristen Hawkes of the University of Utah, Hillard Kaplan of the University of New Mexico and others have shown in their studies of several modern-day hunter-gatherer groups, grandparents routinely contribute economic and social resources to their descendants, increasing both the number of offspring their children can have and the survivorship of those children. Grandparents also reinforce complex social connections—like my grandmother did in telling stories of ancestors that linked me to other relatives in my generation.

Elders transmit other kinds of cultural knowledge, too—from environmental (what kinds of plants are poisonous or where to find water during a drought, for example) to technological (how to weave a basket or knap a stone knife, perhaps). Multigenerational families have more members to hammer home important lessons. Thus, longevity presumably fostered the intergenerational accumulation and transfer of information that encouraged the formation of intricate kinship systems and other social networks.

Increases in longevity would also have translated into increases in population size by adding an age group that was not there in the past and that was still fertile. And large populations are major drivers of new behaviors. In 2009 Adam Powell, then at University College London, and his colleagues published a paper in *Science* showing that population density figures importantly in the maintenance of cultural complexity. They and many other researchers argue that larger populations promoted the development of extensive trade networks, complex systems of cooperation, and material expressions of individual and group identity (jewelry, body paint, and so on). Viewed in that light, the hallmark features of the Upper Paleolithic look as though they might well have been consequences of swelling population size.

Growing population size would have affected our forebears another way, too: by accelerating the pace of evolution. As John Hawks of the University of Wisconsin–Madison has emphasized, more people mean more mutations and opportunities for advantageous mutations to sweep through populations as their members reproduce. This trend may have had an even more striking effect on recent humans than on Upper Paleolithic ones, compounding the dramatic population growth that accompanied the domestication of plants 10,000 years ago.

The relation between adult survivorship and the emergence of sophisticated new cultural traditions was almost certainly a positive feedback process. Initially a by-product of some sort of cultural change, longevity became a prerequisite for the complex behaviors that signal modernity. These innovations in turn promoted the importance and survivorship of older adults, which led to the population expansions that had such profound cultural and genetic effects on our predecessors. Older and wiser, indeed. SA

Rachel Caspari is professor of anthropology at Central Michigan University. Her research focuses on Neandertals, the origin of modern humans and the evolution of longevity.

MORE TO EXPLORE

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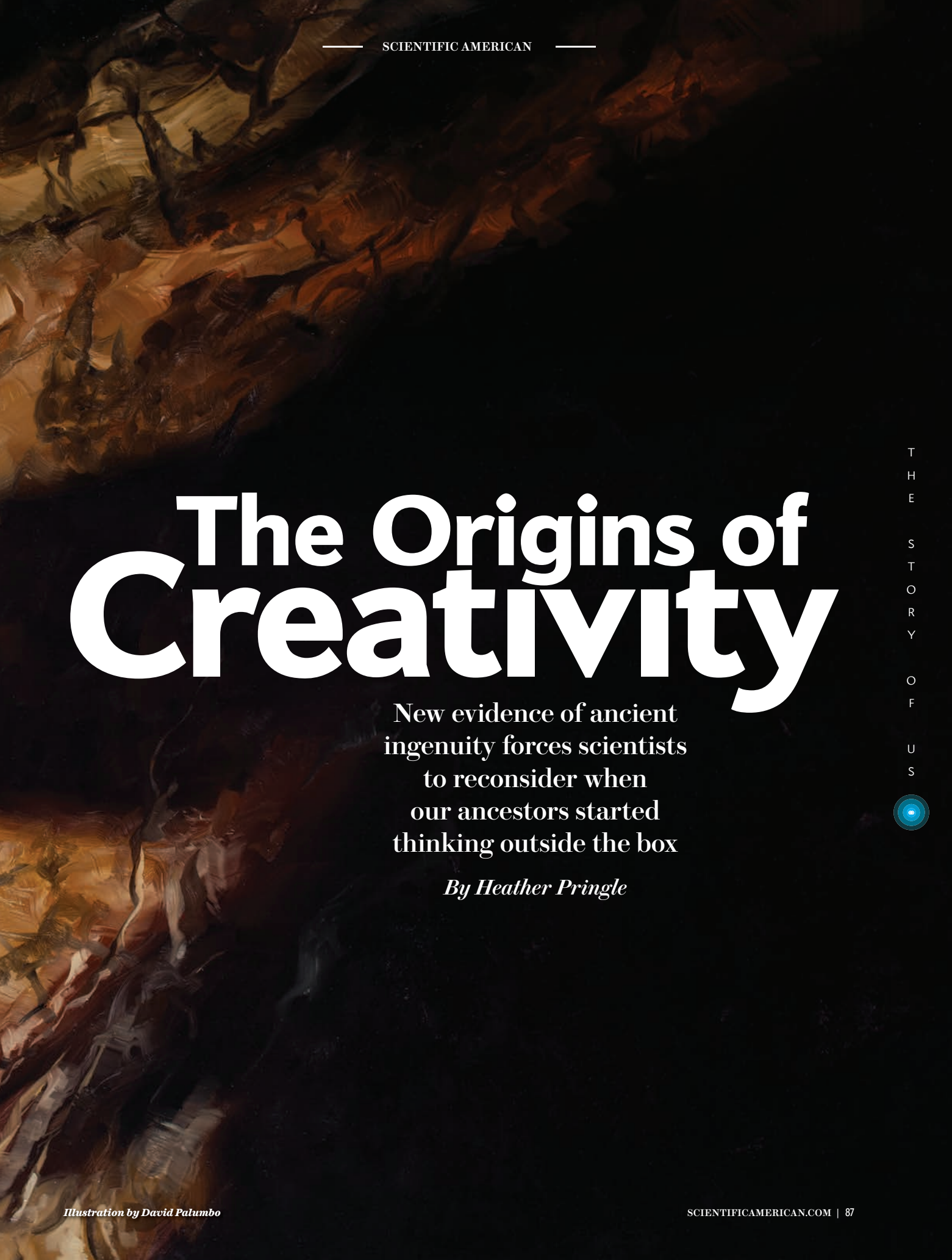


The Origins of Creativity

New evidence of ancient ingenuity forces scientists to reconsider when our ancestors started thinking outside the box

By Heather Pringle

Illustration by David Palumbo

UNSIGNED AND UNDATED, INVENTORY NUMBER 779 HANGS BEHIND THICK glass in the Louvre's brilliantly lit Salle des États. A few minutes after the stroke of nine each morning, except for Tuesdays when the museum remains closed, Parisians and tourists, art lovers and curiosity seekers begin flooding into the room. As their hushed voices blend into a steady hivelike hum, some crane for the best view; others stretch their arms urgently upward, clicking cell-phone cameras. Most, however, tilt forward, a look of rapt wonder on their faces, as they study one of humanity's most celebrated creations: the *Mona Lisa,* by Leonardo da Vinci.

Completed in the early 16th century, the *Mona Lisa* possesses a mysterious, otherworldly beauty quite unlike any portrait that came before it. To produce such a painting, Leonardo developed a new artistic technique he called *sfumato,* or "smoke." Over a period of several years he applied translucent glazes in delicate films—some no more than the thickness of a red blood cell—to the painting, most likely with the sensitive tip of his finger. Gradually stacking as many as 30 of these films one on top of another, Leonardo subtly softened lines and color gradations until it seemed as if the entire composition lay behind a veil of smoke.

The *Mona Lisa* is clearly a work of inventive genius, a masterpiece that stands alongside the music of Mozart, the jewels of Fabergé, the choreography of Martha Graham, and other such classics. But these renowned works are only the grandest manifestations of a trait that has long seemed part of our human hardwiring: the ability to create something new and desirable, the knack of continually improving designs and technologies—from the latest zero-emissions cars made in Japan to the sleekly engineered Falcon 9 rockets from SpaceX. Modern humans, says Christopher S. Henshilwood, an archaeologist at the Universities of Bergen in Norway and the Witwatersrand, Johannesburg, in South Africa, "are inventors of note. We advance and experiment with technology constantly."

Just how we came by this seemingly infinite capacity to create is the subject of intense scientific study: we were not always such whirlwinds of invention. Although our human lineage emerged in Africa around six million years ago, early family members left behind little visible record of innovation for nearly 3.4 million years, suggesting that they obtained plant and animal foods by hand, with tools such as digging or jabbing sticks that did not preserve. Then, at some point, wandering hominins started flaking water-worn cobblestones with hammerstones to produce cutting tools. That was an act of astonishing ingenuity, to be sure, but a long plateau followed—during which very little seems to have happened on the creativity front. Our early ancestors apparently knapped the same style of handheld, multipurpose hand ax for 1.6 million years, with only minor tweaks to the template. "Those tools are really kind of stereotypical," says Sally McBrearty, an archaeologist at the University of Connecticut.

So when did the human mind begin churning with new ideas for technology and art? Until recently, most researchers pointed to the start of the Upper Paleolithic period 40,000 years ago, when *Homo sapiens* embarked on what seemed a sudden, wondrous invention spree in Europe: fashioning shell-bead necklaces, adorning cave walls with geometric signs and paintings of Ice Age animals, and carving and knapping a wide variety of new stone and bone tools. The finds prompted a popular theory proposing that a random genetic mutation at around that time had spurred a sudden leap in human cognition, igniting a creative "big bang."

IN BRIEF

Scientists long thought that early humans were stuck in a creative rut until some 40,000 years ago, when their powers of innovation seemed to explode.

But archaeological discoveries made in recent years have shown that our ancestors had flashes of brilliance far earlier than that.

These findings indicate that the human capacity for innovation emerged over hundreds of thousands of years, driven by both biological and social factors.

FINDINGS

Fermenting Genius

Surprisingly early examples of technological and artistic inventiveness indicate that human creativity simmered for hundreds of thousands of years before reaching a boil around 90,000 to 60,000 years ago in Africa and 40,000 years ago in Europe. Social factors, including an increase in population size, seem likely to have amplified our ancestors' powers of innovation, both by improving the odds that someone in the group would come up with a breakthrough technology and by fostering connectedness between groups that allowed them to exchange ideas. This timeline charts the earliest known evidence of key innovations leading up to the cultural boiling point.

3.4 million years ago
Cut-marked animal bones from Dikika, Ethiopia

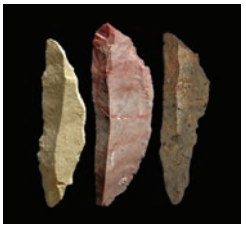
2.6 million years ago
Flaked stone tools from Gona, Ethiopia

1.76 million years ago
Bifacial stone tool from Turkana, Kenya

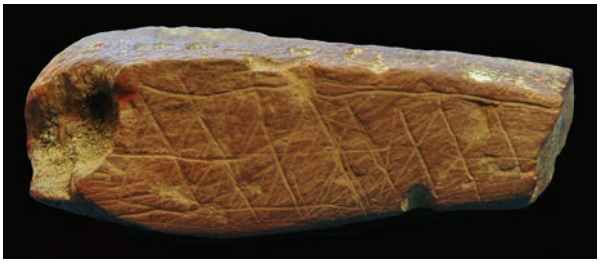
1 million years ago
Burned bone and plant material indicative of controlled fire from Wonderwerk Cave, South Africa

500,000 years ago
Composite tools—in the form of stone points that would have been affixed to wood shafts—from Kathu Pan 1, South Africa

164,000 years ago
Heat-treated stone tools from Pinnacle Point, South Africa



100,000–75,000 years ago
Engraved ocher (iron oxide) from Blombos Cave, South Africa



77,000 years ago
Insect-repellent bedding from Sibudu Cave, South Africa

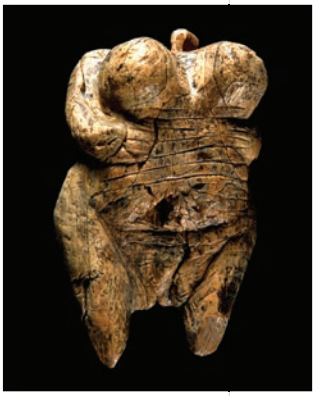
71,000 years ago
Projectile points from Pinnacle Point, South Africa

40,000–30,000 years ago
Sewing needles from Kostenki, Russia

43,000–42,000 years ago
Musical instrument (flute, side and top view) from Geissenklösterle Cave, Germany

41,000–37,000 years ago
Cave art, including hand stencils, from El Castillo, Spain

40,000–35,000 years ago
Figurative art: the Venus of Hohle Fels, Germany



IN ORDER OF TIMELINE: COURTESY OF P. J. TEXIER, © MPK/WTAP; COURTESY OF JAYNE WILKINS *University of Toronto*; COURTESY OF CHRISTOPHER S. HENSHILWOOD *University of Bergen and the Witwatersrand, Johannesburg*; COURTESY OF TOVE; RUTH SMITH AND SIMEN ØSTMO; COURTESY OF J. LIPTÁK, © UNIVERSITY OF TÜBINGEN; COURTESY OF D. AND G. VON PETZINGER; COURTESY OF H. JENSEN, © UNIVERSITY OF TÜBINGEN

THE STORY OF US

1

New evidence, however, has cast grave doubt on the mutation theory. Over the past decade or so archaeologists have uncovered far older evidence of art and advanced technology, suggesting that the human capacity to cook up new ideas evolved much earlier than previously thought—even before the emergence of *H. sapiens* 200,000 years ago. Yet although our capacity for creativity sparked early on, it then smoldered for millennia before finally catching fire in our species in Africa and Europe. The evidence seems to indicate that our power of innovation did not burst into existence fully formed late in our evolutionary history but rather gained steam over hundreds of thousands of years, fueled by a complex mix of biological and social factors.

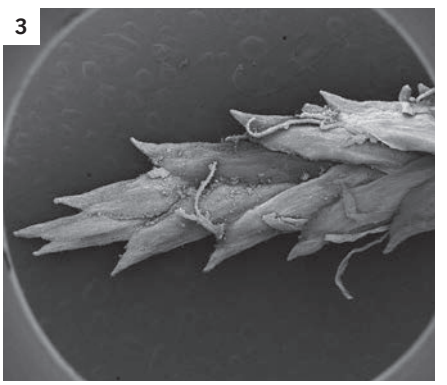
Exactly when did humankind begin thinking outside the box, and what factors converged to ultimately fan our brilliant creative fire? Understanding this scenario requires following a detective story composed of several strands of evidence, starting with the one showing that the biological roots of our creativity date back much further than scientists once thought.

MOTHER OF INVENTION

ARCHAEOLOGISTS HAVE LONG VIEWED the use of symbols as the single most important indicator of modern human cognition, in large part because it attests to a capacity for language—a hallmark human trait. Thus, the geometric signs and the spectacular cave art of the Upper Paleolithic clearly signal the presence of people who thought as we do. But more recently, experts have begun searching for hints of other kinds of modern behavior and its antecedents in the archaeological record—and coming up with fascinating clues.

Archaeologist Lyn Wadley of the University of the Witwatersrand, Johannesburg, has spent much of her career studying ancient cognition, research that led her in the 1990s to open excavations at Sibudu Cave, some 40 kilometers north of Durban, South Africa. At that same site, about five years ago, she and her team discovered a layer of strange, white, fibrous plant material there. To Wadley, the pale, brittle mash looked like ancient bedding—rushes and other plants that later people often scattered on the ground for sitting and sleeping on. But the layer could also have formed from wind-borne leaf litter. The only way to tell one from the other was to encase the entire layer in a protective plaster jacket and take it back to the laboratory. "It took us three weeks to make all that plaster," Wadley recounts, "and I was really grumpy the whole time. I kept wondering, 'Am I wasting three weeks in the field?'"

COURTESY OF LYN WADLEY *University of the Witwatersrand, Johannesburg*



ANCIENT WISDOM: Painstaking excavation of Sibudu Cave in South Africa (*1*) has yielded evidence that its inhabitants made bedding (*2*) from insect-repellent plants (*3*) some 77,000 years ago—50,000 years earlier than the previously known examples of this technology.

But Wadley's gamble paid off richly. In 2011 she and her colleagues reported in *Science* that Sibudu's occupants selected leaves from just one of many woody species in the area to make bedding 77,000 years ago—nearly 50,000 years earlier than previously reported examples. What most surprised Wadley, however, was the occupants' sophisticated knowledge of the local vegetation. Analysis showed that the chosen leaves came from *Cryptocarya woodii,* a tree containing traces of natural insecticides and larvicides effective against the mosquitoes that carry deadly disease today. "And that's very handy to have in your bedding, particularly if you live near a river," Wadley observes.

The creative minds at Sibudu did not stop there, however. They most likely devised snares to capture small antelopes, whose remains litter the site, and crafted bows and arrows to bring down more dangerous prey, judging from the sizes, shapes and wear patterns of several stone points from the cave. Moreover, Sibudu's hunters concocted various valuable new chemical compounds. By shooting a high-energy beam of charged particles at dark residues on stone points from the cave, Wadley's team detected multi-ingredient glues that once fastened the points to wood hafts. She and her colleagues then set about experimentally replicating these adhesives, mixing ocher particles of different sizes with plant gums and heating the mixtures over wood fires. Publishing the results in *Science,* the team concluded that Sibudu's occupants were very likely "competent chemists, alchemists and pyrotechnologists" by 70,000 years ago.

Elsewhere in southern Africa, researchers have recently turned up traces of many other early inventions. The hunter-gatherers who inhabited Blombos Cave between 100,000 and 72,000 years ago, for example, engraved patterns on chunks of ocher; fashioned bone awls, perhaps for tailoring hide clothing; adorned themselves with strands of shimmering shell beads; and created an artists' studio where they ground red ocher and stored it in the earliest known containers, made from abalone shells. Farther west, at the site of Pinnacle Point, people engineered the stone they worked with 164,000 years ago, heating a low-grade, local rock known as silcrete over a controlled fire to transform it into a lustrous, easily knappable material. "We are seeing behaviors that we didn't even dream about 10 years ago," Henshilwood remarks.

Moreover, technological ingenuity was not the sole preserve of modern humans: other hominins possessed a creative streak, too. In northern Italy a research team headed by University of Florence archaeologist Paul Peter Anthony Mazza discovered that our near kin, the Neandertals, who first emerged in Europe some

300,000 years ago, concocted a birch bark–tar glue to fasten stone flakes to wood handles, fabricating hafted tools some 200,000 years ago. Likewise, a study published in 2012 in *Science* concluded that stone points from the site of Kathu Pan 1 in South Africa once formed the lethal tips of 500,000-year-old spears, presumably belonging to *Homo heidelbergensis,* the last common ancestor of Neandertals and *H. sapiens.* And at Wonderwerk Cave in South Africa, an ancient layer containing plant ash and bits of burned bone suggests that an even earlier hominin, *Homo erectus,* learned to kindle fires for warmth and protection from predators as early as one million years ago.

Even our very distant ancestors were capable on occasion of coining new ideas. At two sites near the Kada Gona River in Ethiopia, a team led by paleoanthropologist Sileshi Semaw of Indiana University Bloomington found stone tools—2.6-million-year-old choppers knapped by *Australopithecus garhi* or one of its contemporaries, likely for stripping meat from animal carcasses. Such tools look crude to us, a far cry from the smartphones, laptops and tablets of today. "But when the world consisted solely of naturally formed objects, the capacity to imagine something and turn it into a reality may well have seemed almost magical," wrote cognitive scientist Liane Gabora of the University of British Columbia and psychologist Scott Barry Kaufman, now at the University of Pennsylvania, in a chapter appearing in *The Cambridge Handbook of Creativity* (Cambridge University Press, 2010).

"IT'S NOT HOW SMART YOU ARE. IT'S HOW WELL CONNECTED YOU ARE."
—Mark Thomas, University College London

COGNITION AND CREATION

YET IMPRESSIVE as these early flashes of creativity are, the great disparity in the depth and breadth of innovation between modern humans and our distant forebears demands an explanation. What changes in the brain set our kind apart from our predecessors? By poring over three-dimensional scans of ancient hominin braincases and by examining the brains of our nearest living evolutionary kin—chimpanzees and bonobos, whose ancestors branched off from our lineage some six million years ago—researchers are beginning to unlock this puzzle. Their data show just how extensively human gray matter evolved over time.

Generally speaking, natural selection favored large brains in humans. Whereas our australopithecine kin possessed an estimated mean cranial capacity of 450 cubic centimeters, roughly that of some chimpanzees, *H. erectus* more than doubled that capacity by 1.6 million years ago, with a mean of 930 cubic centimeters. And by 100,000 years ago *H. sapiens* had a mean capacity of 1,330 cubic centimeters. Inside this spacious braincase, an estimated 100 billion neurons processed information and transmitted it along nearly 165,000 kilometers of myelinated nerve fibers and across some 0.15 quadrillion synapses. "And if you look at what this correlates with in the archaeological record," says Dean Falk, a paleoneurologist at Florida State University, "there does seem to be an association between brain size and technology or intellectual productivity."

But size was not the only major change over time. At the University of California, San Diego, biological anthropologist Katerina Semendeferi studies a part of the brain known as the prefrontal cortex, which appears to orchestrate thought and action to accomplish goals. Examining this region in modern humans and in both chimpanzees and bonobos, Semendeferi and her colleagues discovered that several key subareas underwent a major reorganization during hominin evolution. Brodmann area 10, for example—which is implicated in bringing plans to fruition and organizing sensory input—nearly doubled in volume after chimpanzees and bonobos branched off from our human lineage. Moreover, the horizontal spaces between neurons in this subarea widened by nearly 50 percent, creating more room for axons and dendrites. "This means that you can have more complicated connections and ones that go farther away, so you can get more complex and more synthetic communication between neurons," Falk comments.

Pinpointing just how a bigger, reorganized brain spurred creativity is a tricky business. But Gabora thinks that psychological studies of creative people today supply a key clue. Such individuals are excellent woolgatherers, she explains. When tackling a problem, they first let their minds wander, allowing one memory or thought to spontaneously conjure up another. This free association encourages analogies and gives rise to thoughts that break out of the box. Then, as these individuals settle on a vague idea for a solution, they switch to a more analytic mode of thought. "They zero in on only the most relevant properties," Gabora says, and they start refining an idea to make it workable.

In all likelihood, Gabora notes, a bigger brain led to a greater ability to free-associate. More stimuli could be encoded in a brain made up of many billions of neurons. In addition, more neurons could participate in the encoding of a particular episode, leading to a finer-grained memory and more potential routes for associating one stimulus with another. Imagine, Gabora says, that a hominin brushes against a spiny shrub and sharp thorns tear its flesh. An australopithecine might encode this episode very simply—as a minor pain and as an identifiable feature of the shrub. But *H. erectus,* with its larger assembly of neurons, could conceivably encode many aspects of the episode. Then, when this hominin begins hunting, its need to kill prey might activate all memory locations encoding torn flesh, bringing to mind the encounter with the sharp pointed thorns. That memory, in turn, could inspire a fresh idea for a weapon: a spear with a sharp pointed tip.

But large-brained hominins could not afford to linger too long in an associative state in which one thing immediately reminded them of a flood of other things, both important and inconsequential. Their survival depended mostly on analytic thought—the default mode. So our ancestors had to develop a way of switching smoothly from one mode to another by subtly altering concentrations of dopamine and other neurotransmitters.

Gabora now hypothesizes that *H. sapiens* needed tens of thousands of years to fine-tune this mechanism before they could reap the full creative benefit of their large brains, and she and her students are testing these ideas on an artificial neural network. Through a computer model, they simulate the brain's ability to switch between the analytic and associative mode to see how it could help someone break out of a cognitive rut and see things in a new way. "Just having more neurons isn't enough," Gabora asserts. "You have to be able to make use of all that extra gray

matter." Once that final piece of the biological puzzle fell into place—perhaps a little more than 100,000 years ago—the ancestral mind was a virtual tinder box, awaiting the right social circumstances to burst into flame.

BUILDING ON BRILLIANCE

IN THE AUTUMN OF 1987 two researchers, both then at the University of Zurich—Christophe and Hedwige Boesch—observed a behavior they had never seen before in a group of chimpanzees foraging for food in Tai National Park in Ivory Coast. Near a ground nest belonging to a species of driver ants, a female stopped and picked up a twig. She dipped one end into the loose soil covering the nest's entrance and waited for the colony's soldier ants to attack. When the dark swarm had advanced nearly 10 centimeters up the twig, the female chimpanzee plucked it from the nest and deftly rolled it toward her mouth, snacking on the ants. She then repeated the process until she had eaten her fill.

Chimpanzees are highly adept at using a wide range of tools—cracking open nuts with stones, sponging up water from tree hollows with leaves and unearthing nutritious plant roots with digging sticks. But they seem unable to build on this knowledge or to craft ever more advanced technology. "Chimps can show other chimps how to hunt termites," Henshilwood says, "but they don't improve on it, they don't say, 'Let's do it with a different kind of probe'—they just do the same thing over and over." Modern humans, in contrast, suffer from no such limitations. Indeed, we daily take the ideas of others and put our own twist on them, adding one modification after another, until we end up with something new and very complex. No one individual, for example, came up with all the intricate technology embedded in a laptop computer: such technological achievements arise from the creative insights of generations of inventors.

Anthropologists call this knack of ours cultural ratcheting. It requires, first and foremost, the ability to pass on knowledge from one individual to another or from one generation to the next, until someone comes along with an idea for an improvement.

In a 2012 study published in *Science* by Lewis Dean, a behavioral primatologist at the University of St. Andrews in Scotland, and four colleagues revealed why human beings can do this and chimpanzees and capuchin monkeys cannot. Dean and his team designed an experimental puzzle box, with three sequential and incrementally difficult levels: then they presented it to groups of chimps in Texas, capuchin monkeys in France and nursery schoolchildren in England. Only one of the 55 nonhuman primates—a chimp—reached the highest level after more than 30 hours of trying. The children, however, fared far better. Unlike the groups of monkeys, the children worked collaboratively—talking among themselves, offering encouragement and showing one another the right way to do things. After two and a half hours, 15 of the 35 children had reached level three.

Equipped with these social skills and cognitive abilities, our ancestors could readily transmit knowledge to others—a key prerequisite for cultural ratcheting. Yet something else was needed to propel the ratcheting process and push *H. sapiens* to new creative heights in Africa some 90,000 to 60,000 years ago and in Europe 40,000 years ago. Mark Thomas, an evolutionary geneticist at University College London, thinks this push came from demography. His premise is simple. The larger a hunter-gatherer group is, the greater the chances are that one member will dream up an idea that could advance a technology. Moreover, individuals in a large group who frequently rubbed shoulders with neighbors had a better chance of learning a new innovation than those in small, isolated groups. "It's not how smart you are," Thomas says. "It's how well connected you are."

To test these ideas, Thomas and two colleagues developed a computer model to simulate the effects of demography on the ratcheting process. With genetic data from modern Europeans, the team estimated the size of modern human populations in Europe at the beginning of the Upper Paleolithic, when evidence of human creativity started to spike, and calculated the population density. Then the researchers examined African populations over time, simulating their growth and patterns of migratory activity. Their model showed that African populations reached the same density as the early Upper Paleolithic Europeans around 101,000 years ago, just before innovation began to take off in sub-Saharan regions, according to the archaeological record. It also showed that large social networks actively spur human creativity.

Archaeological evidence published in 2012 in *Nature* sheds light on the tech renaissance that followed the rise of population density in southern Africa. Some 71,000 years ago at Pinnacle Point, *H. sapiens* devised and passed down to others a complex technological recipe to make lightweight stone blades for projectile weapons—cooking silcrete to a specific temperature to improve its flaking qualities, knapping the finished material into blades little more than a couple of centimeters long, and mounting them on wood or bone shafts with homemade glue. "Like viruses," note archaeologists Fiona Coward of Bournemouth University and Matt Grove of the University of Liverpool in England in a paper published in 2011 in *PaleoAnthropology,* "cultural innovations need very particular social conditions to spread—most notably… large connected populations who can 'infect' one another."

Which brings us to the jostling, teeming, intimately linked world we live in today. Never before have humans crowded together in such massive cities, accessing vast realms of knowledge with a click of the keyboard and sharing new concepts, new blueprints and designs across the sprawling social networks of the World Wide Web. And never before has the pace of innovation accelerated so dramatically, filling our lives with new fashions, new electronics, new cars, new music, new architecture.

Half a millennium after Leonardo da Vinci conceived of his most celebrated work, we marvel at his inventive genius—a genius built on the countless ideas and inventions of a lineage of artists stretching back into the Paleolithic past. And even now a new crop of artists gaze at the *Mona Lisa* with an eye to turning it into something fresh and dazzlingly creative. The human chain of invention remains unbroken, and in our superbly connected world, our singular talent to create races on ahead of us. SA

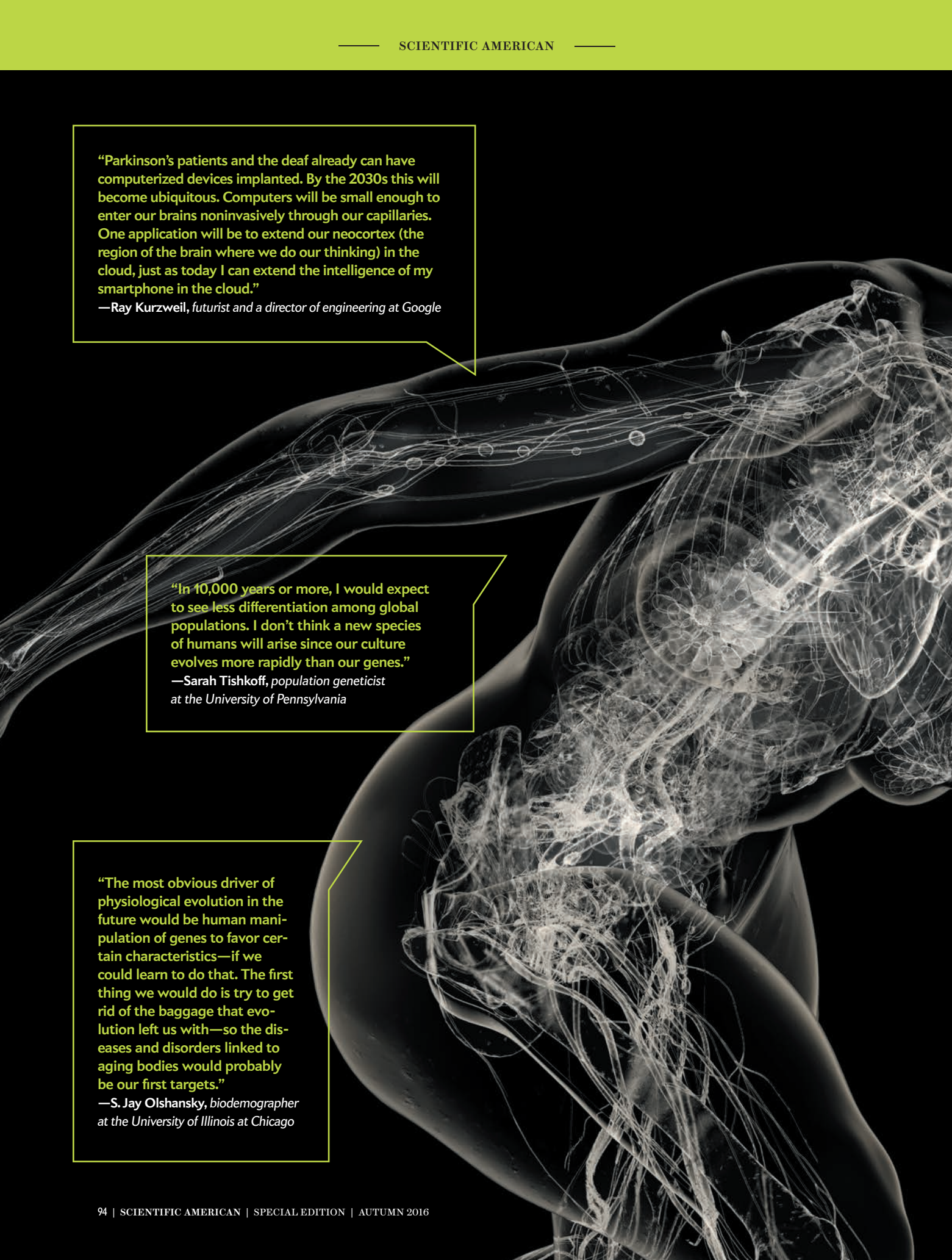
Heather Pringle is a Canadian science writer and a contributing correspondent for *Science*.

MORE TO EXPLORE

Middle Stone Age Bedding Construction and Settlement Patterns at Sibudu, South Africa. Lyn Wadley et al. in *Science*, Vol. 334, pages 1388–1391; December 9, 2011.
Hominin Paleoneurology: Where Are We Now? Dean Falk in *Progress in Brain Research*, Vol. 195, pages 255–272; 2012.

scientificamerican.com/magazine/sa

"Parkinson's patients and the deaf already can have computerized devices implanted. By the 2030s this will become ubiquitous. Computers will be small enough to enter our brains noninvasively through our capillaries. One application will be to extend our neocortex (the region of the brain where we do our thinking) in the cloud, just as today I can extend the intelligence of my smartphone in the cloud."
—Ray Kurzweil, *futurist and a director of engineering at Google*



"In 10,000 years or more, I would expect to see less differentiation among global populations. I don't think a new species of humans will arise since our culture evolves more rapidly than our genes."
—Sarah Tishkoff, *population geneticist at the University of Pennsylvania*

"The most obvious driver of physiological evolution in the future would be human manipulation of genes to favor certain characteristics—if we could learn to do that. The first thing we would do is try to get rid of the baggage that evolution left us with—so the diseases and disorders linked to aging bodies would probably be our first targets."
—S. Jay Olshansky, *biodemographer at the University of Illinois at Chicago*

3

Where We Are Going

WE ASKED leading scientists how they think humans will evolve in the future. Here is what they had to say. For more on the future of humanity, read on; also, visit ScientificAmerican.com/report/future-of-humanity

"Evolution is incessant, and humans, like every other life-form on earth, are evolving and will continue to evolve; however, nobody knows what humans will become other than maybe going extinct. Evolution has its own ways that no one can predict for sure."
—Yohannes Haile-Selassie, *paleoanthropologist at the Cleveland Museum of Natural History*

Illustration by Bryan Christie, Reporting by Kevin Schultz

The Networked Primate

For the first time in the history of our species, we are never alone and never bored. Have we lost something fundamental about being human?

Interview by Mark Fischetti

CHANCES ARE THAT YOU HAVE A SMARTPHONE, TWITTER and Instagram accounts, and a Facebook page and that you have found yourself ignoring a friend or family member who is in the same room as you because you are totally engrossed in your social technology. That technology means never having to feel alone or bored. Yet ironically, it can make us less attentive to the people closest to us and even make it hard for us to simply be with ourselves. Many of us are afraid to make this admission. "We're still in a romance with these technologies," says Sherry Turkle of the Massachusetts Institute of Technology. "We're like young lovers who are afraid that talking about it will spoil it." Turkle has interviewed, at length, hundreds of individuals of all ages about their interactions with smartphones, tablets, social media, avatars and robots. Unlike previous disruptive innovations such as the printing press or television, the latest "always on, always on you" technology, she says, threatens to undermine some basic human strengths that we need to thrive. In the conversation that follows, which has been edited for space, Turkle explains her concerns, as well as her cautious optimism that the youngest among us could actually resolve the challenges.

IN BRIEF

WHO
SHERRY TURKLE

VOCATION
Sociologist

WHERE
Massachusetts Institute of Technology

RESEARCH FOCUS
How people interact with technology and how that affects human relationships.

BIG PICTURE
Social networking is making us less social.

Illustration by Martin O'Neill

Like
Like
LIKE.....
LIKE.....
LIKE.....
POKE
300 FRIENDS

SCIENTIFIC AMERICAN:
What concerns you most about our constant interaction with our social technologies?

TURKLE: One primary change I see is that people have a tremendous lack of tolerance for being alone. I do some of my fieldwork at stop signs, at checkout lines at supermarkets. Give people even a second, and they're doing something with their phone. Every bit of research says people's capacity to be alone is disappearing. What can happen is that you lose that moment to have a daydream or to cast an eye inward. Instead you look to the outside.

Is that an issue for individuals of all ages?

Yes, but children especially need solitude. Solitude is the precondition for having a conversation with yourself. This capacity to be with yourself and discover yourself is the bedrock of development. But now, from the youngest age—even two, or three, or four—children are given technology that removes solitude by giving them something externally distracting. That makes it harder, ironically, to form true relationships.

Maybe people just don't want to be bored.

People talk about never needing to have a lull. As soon as it occurs, they look at the phone; they get anxious. They haven't learned to have conversations or relationships, which involve lulls.

Are we valuing relationships less, then?

People start to view other people in part as objects. Imagine two people on a date. "Hey, I have an idea. Instead of our just looking at each other face-to-face, why don't we each wear Google Glass, so if things get a little dull, I can just catch up on my e-mail? And you won't know." This disrupts the family, too. When Boring Auntie starts to talk at the family dinner table, her little niece pulls out her phone and goes on Facebook. All of a sudden her world is populated with snowball fights and ballerinas. And dinner is destroyed. Dinner used to be the utopian ideal of the American family having a canonical three-generation gathering.

What about people who take their phones to bed? They're asleep, so why would they feel alone?

I have interviewed enough middle school and high school kids: "So tell me, do you answer your texts in the middle of the night?" "Oh, yeah." I call it "I share, therefore I am," as a style of being.

If you're sharing in the middle of the night and responsive to people in the middle of the night, you're in a different zone. And all these people feel responsible to respond. The expectation is constant access. Everyone is ready to call in the advice and the consent of their peers. I did a case study of a young woman who has 2,000 followers on Instagram. She'll ask about a problem at 9:00 at night, and at 2:00 in the morning she's getting responses, and she's awake to get those responses. This is 2:00 in the morning for a lot of kids.

Where does this lead for someone who lives that way?

If you don't call a halt to it, I think you don't fully develop a sense of an autonomous self. You're not able to be in personal relationships, business relationships, because you don't feel fully competent to handle major things on your own. You run into trouble if you're putting everything up, ultimately, for a vote.

You're crowdsourcing your life.

You're crowdsourcing major decisions. I hope it's likely, however, that a person reaches a point where they're on a job—they're not twentysomething, they're thirtysomething—and this starts to become less comfortable, and they develop emotional skills that they really haven't worked on.

What about our interactions with automated personalities and robots?

When we started looking at this in the 1970s, people took the position that even if simulated thinking might be thinking, simulated feeling was not feeling. Simulated love was never love. But that's gone away. People tell me that if Siri [the iPhone voice] could fool them a little better, they'd be happy to talk to Siri.

Isn't that like the movie *Her*?

Absolutely. The current position seems to be that if there's a robot that could fool me into thinking that it understands me, I'm good to have it as a companion. This is a significant evolution in what we ask for in our interactions, even on intimate matters. I see it in kids. I see it in grown-ups. The new robots are designed to make you feel as though you're understood. Yet nobody is pretending that any of them understands anything.

What line does that cross—that there's no empathy?

There's no authentic exchange. You're saying empathy is not important to the feeling of being understood. And yet I interviewed a woman who said to me that she's okay with a robot boyfriend. She wants one of these sophisticated Japanese robots. I looked at her and said, "You know that it doesn't understand you." She said, "Look, I just want civility in the house. I just want something that will make me feel not alone."

People are also good with a robot that could stand in as a companion for an older person. But I take a moral position here because older people deserve to tell the story of their life to someone who understands what a life is. They've lost spouses; they've lost children. We're suggesting they tell the story of their life to something that has no idea what a life is or what a loss is.

It's crucial to understand that this changing interaction is not just a story about technology. It's a story about how we are evolving when we're faced with something passive. I hope we're going to look closer at people's willingness to project humanity onto a robot and to accept a facade of empathy as the real thing because I think that such interactions are a dead end. We want more from technology and less from each other? Really?

Do avatars and virtual reality present the same issues?

In these cases, we are moving from life to the mix of your real life and your virtual life. One young man put it very succinctly: "Real life is just one window, and it's not necessarily my best one." People forgot about virtual reality for a while, but the acquisition of Oculus by Facebook raised it again—Mark Zuckerberg's fantasy that you will meet up with your friends in a virtual world

PAGE 96: ERIK JACOBS New York Times/*Redux Pictures (Turkle)*

where everybody looks like Angelina Jolie and Brad Pitt, you live in a beautiful home, and you present only what you want to present. We're evolving toward thinking of that as a utopian image.

But skeptics say your avatar is not different from the real you.
Well, we do perform all the time. I'm trying to do my best Sherry Turkle right now. But it's a little different from me hanging out in my pajamas. What's different with an avatar or on Facebook is that you get to edit. A woman posts a photo of herself and then works on the color and background and lighting. Why? Because she wants it a certain way. We've never before been able to have it the way we wanted it. And now we can. People love that.

I asked an 18-year-old man, "What's wrong with conversation?" He said, "It takes place in real time. You can't control what you're going to say." It was profound. That's also why a lot of people like to do their dealings on e-mail—it's not just the time shifting; it's that you basically can get it right.

One reason for the rise of humans is that functioning in groups gives each member a better chance to succeed. Will the move toward living online undermine those benefits?
Oh, this is the question before us. Are we undermining, or are we enhancing our competitive advantage? A lot of my colleagues would say we're enhancing it. The Internet is giving us new ways of getting together, forming alliances. But I think we are at a point of inflection. While we were infatuated with the virtual, we dropped the ball on where we actually live. We need to balance how compelling the virtual is with the realities that we live in our bodies and on this planet. It is so easy for us to look the other way. Are we going to get out there and make our real communities what they should be?

Your critics say there's nothing to worry about because this "new technology" situation is not really new. We went through this with television—you know, TV is there to watch your kids so you don't have to.
First of all, television can be a group exercise. I grew up in a family that sat around a TV and watched it together, fought about what was on the TV together, commented on it together. But when everybody watches their own show in their own room, so to speak, that stops. Technology that is always on and always on you—that is a quantum leap. I agree that there have been quantum leaps before: the book. The difference with "always on," however, is that I really don't have a choice.

You mean, you could turn off the TV and still function.
I cannot live my professional life or my personal life without my phone or my e-mail. My students can't even obtain their syllabus without it. We don't have an opt-out option from a world with this technology. The question is, How are we going to live a more meaningful life with something that is always on and always on you? And wait until it's in your ear, in your jacket, in your glasses.

So how do we resolve that?
It's going to develop as some sort of common practice. I think companies will get involved, realizing that it actually isn't good for people to be constantly connected. Our etiquette will get involved; today if I get a message and don't get back to people in 24 hours, they're worried about me, or they're mad that I haven't replied. Why? I think we will change our expectation of having constant access.

Any suggestions for how we can get started?
One argument I make is that there should be sacred spaces: the family dinner table, the car. Make these the places for conversation because conversation is the antidote to a lot of the issues I'm describing. If you're talking to your kids, if you're talking to your family, if you're talking to a community, these negative effects don't arise as much.

And we should be talking more about the technologies?
My message is not antitechnology. It's pro conversation and pro the human spirit. It's really about calling into questions our dominant culture of more, better, faster. We need to assert what we need for our own thinking, for our own development, and for our relationships with our children, with our communities, with our intimate partners. As for the robots, I'm hoping that people will realize that what we're really disappointed in is ourselves. It's so upsetting to me. We're basically saying that we're not offering one another the conversation and the companionship. That, really, is the justification for talking to a robot that you know doesn't understand a word you're saying. We are letting each other down. It's not about the robots. It's about us.

So who is going to stop this train we are on?
The most optimistic thing I see is the young people who have grown up with this technology but aren't smitten by it, who are willing to say, "Hold on a second." They see the ways in which it's undermined life at school and life with their parents. This is where I'm guardedly hopeful.

I have so many examples of children who will be talking with their parents; something will come up, and the parent will go online to search, and the kid will say, "Daddy, stop Googling. I just want to talk to you." When I go to the city park, I see kids go to the top of the jungle gym and call out, "Mommy, Mommy!" and they're being ignored. They object to being ignored when they're five, eight or nine. But when I interview these kids when they're 13, 14 or 15, they become reflective. They say, "I'm not going to bring up my children the way I'm being brought up." They're going to have rules, like no phones at dinner.

I also see evidence that dealing with some of this technology is feeling to them like work—the whole notion that you have to constantly keep up your Facebook profile. So I think there's every possibility that the children will lead us. They see the costs. They think, "I don't have to give up this technology, but maybe I could be a little smarter about it." SA

Mark Fischetti is a senior editor at *Scientific American*.

MORE TO EXPLORE

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scientificamerican.com/magazine/sa

Still Evolving

(After All These Years)

For 30,000 years our species has been changing remarkably quickly. And we're not done yet

By John Hawks

IN BRIEF

Some scientists and science communicators have claimed that humans are no longer subject to natural selection and that human evolution has effectively ceased.

In fact, humans have evolved rapidly and remarkably in the past 30,000 years. Straight black hair, blue eyes and lactose tolerance are all examples of relatively recent traits.

Such rapid evolution has been possible for several reasons, including the switch from hunting and gathering to agrarian-based societies, which permitted human populations to grow much larger than before. The more people reproduce within a population, the higher the chance of new advantageous mutations.

Humans will undoubtedly continue to evolve into the future. Although it may seem that we are headed toward a cosmopolitan blend of human genes, future generations will likely be striking mosaics of our entire evolutionary past.

Illustration by Christian Northeast

HUMANS ARE WILLFUL CREATURES. NO OTHER SPECIES ON THE PLANET HAS gained so much mastery over its own fate. We have neutralized countless threats that once killed us in the millions: we have learned to protect ourselves from the elements and predators in the wild; we have developed cures and treatments for many deadly diseases; we have transformed the small gardens of our agrarian ancestors into the vast fields of industrial agriculture; and we have dramatically increased our chances of bearing healthy children despite all the usual difficulties.

Many people argue that our technological advancement—our ability to defy and control nature—has made humans exempt from natural selection and that human evolution has effectively ceased. There is no "survival of the fittest," the argument goes, if just about everyone survives into old age. This notion is more than just a stray thought in the public consciousness. Professional scientists such as Steven Jones of University College London and respected science communicators such as David Attenborough have also declared that human evolution is over.

But it is not. We have evolved in our recent past, and we will continue to do so as long as we are around. If we take the more than seven million years since humans split from our last common ancestor with chimpanzees and convert it to a 24-hour day, the past 30,000 years would take about a mere six minutes. Yet much has unfolded during this last chapter of our evolution: vast migrations into new environments, dramatic changes in diet and a more than 1,000-fold increase in global population. All those new people added many unique mutations to the total population. The result was a pulse of rapid natural selection. Human evolution is not stopping. If anything, it is accelerating.

AN ANTHROPOLOGICAL LEGACY

SKELETONS OF ANCIENT PEOPLE have long suggested that humans evolved certain traits swiftly and recently. About 11,000 years ago, as people started to transition from hunting and gathering to farming and cooking, human anatomy changed. Ten thousand years ago, for example, people's teeth averaged more than 10 percent larger in Europe, Asia and North Africa than today. When our ancestors started to eat softer cooked foods that required less chewing, their teeth and jaws shrank, bit by bit, each generation.

Although anthropologists have known about such traits for decades, only in the past dozen years has it become clear just how new they really are. Studies of human genomes have made the recent targets of selection highly visible to us. It turns out, for example, that descendants of farmers are much more likely to have a greater production of salivary amylase, a key enzyme that breaks down starches in food. Most people alive today have several copies of the gene that codes for amylase, *AMY1*. Modern hunter-gatherers—such as the Datooga in Tanzania—tend to have far fewer copies than people whose ancestors came from farming populations, whether they live in Africa, Asia or the Americas. Getting a jump on starch processing at the point of entry seems to have been an advantage for ancient farmers wherever they adopted starchy grains.

Another dietary adaptation is one of the best-studied examples of recent human evolution: lactose tolerance. Nearly everyone in the world is born with the ability to produce the enzyme lactase, which breaks down the milk sugar lactose and makes it easier to extract energy from milk—essential for the survival of a suckling child. Most people lose this ability by adulthood. At least five different times in our recent evolutionary past, as people started to discover dairy, a genetic mutation arose to lengthen the activity of the lactase gene. Three of the mutations originated in different parts of sub-Saharan Africa, where there

HUMAN EVOLUTION

Recent Traits

Many commonplace features of human biology are relatively new. Blue eyes, straight, thick black hair, the ability to digest milk in adulthood and some mutations that lightened skin all emerged in the past 30,000 years.

ANTHONY LEE *Getty Images (eye)*; ANDREAS KUEHN *Getty Images (hair)*; DAITOZEN *Getty Images (milk)*

is a long history of cattle herding. Another one of the five genetic tweaks is common in Arabia and seems to have sprung up in ancient populations of camel and goat herders.

The fifth and most common variant of the mutation that keeps the lactase gene turned on in adulthood is found today in human populations stretching from Ireland to India, with its highest frequencies across northern Europe. The mutation originated in a single individual 7,500 years ago (give or take a few thousand years). In 2011 scientists analyzed DNA recovered from Ötzi the Iceman, who was naturally mummified about 5,500 years ago in northern Italy. He did not have the lactose-tolerance mutation, a hint that it had not yet become common in this region thousands of years after its initial origin. In following years, researchers sequenced DNA extracted from the skeletons of farmers who lived in Europe more than 5,000 years ago. None carried the lactase mutation. Yet in the same region today, the lactase-persistence mutation occurs in hundreds of millions of people—more than 75 percent of the gene pool. This is not a paradox but the mathematical expectation of natural selection. A new mutation under selection grows exponentially, taking many generations to become common enough to notice in a population. But once it becomes common, its continued growth is very rapid and ultimately dominates.

THE SHALLOWNESS OF RACES

WHAT IS PERHAPS MOST EXTRAORDINARY about our recent evolution is how many common physical features are completely new to human anatomy. The thick, straight black hair shared by most East Asians, for example, arose only within the past 30,000 years, thanks to a mutation in a gene called *EDAR,* which is crucial for orchestrating the early development of skin, hair, teeth and nails. That genetic variant traveled with early colonizers of the Americas, all of whom share an evolutionary past with East Asians.

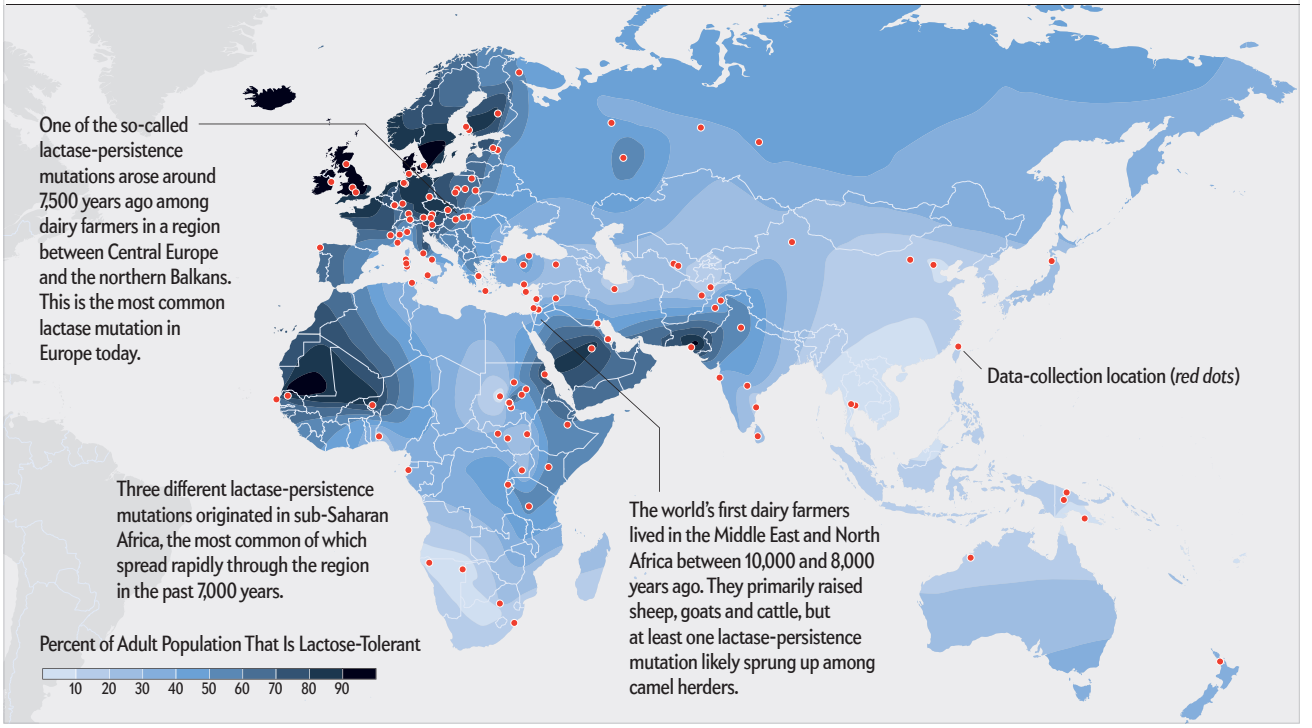
In fact, the overall evolutionary history of human skin, hair and eye pigmentation is surprisingly shallow. In the earliest stages of our evolution, all our ancestors had dark skin, hair and eyes. Since this initial state, dozens of genetic changes have lightened these features to some extent. A few of these changes are ancient variations present within Africa but more common elsewhere in the world. Most are new mutations that have emerged in one population or another: a change in a gene named *TYRP1,* for instance, that makes certain Solomon Islanders blond; the *HERC2* mutation that results in blue eyes; changes to *MC1R* that causes red hairs to sprout instead of black ones; and a mutation in the *SLC24A5* gene that lightens skin color and that is now found in up to 95 percent of Europeans. As in the case of lactase, ancient DNA is giving clear information about the antiquity of such mutations. Blue eyes seem to have appeared in people who lived more than 9,000 years ago, but the massive change to *SLC24A5* is not found in the DNA of ancient skeletons from the same time period. Skin, hair and eye color evolved with stunning speed.

Variations in pigmentation are some of the most obvious differences between the races and, in some ways, the easiest to study. Scientists have also investigated much odder and less evident features of human anatomy. Consider the variations of earwax. Most people in the world today have sticky earwax. In contrast, many East Asians have dry, flaky earwax that does not stick together. Anthropologists have known about this variation for more than 100 years, but geneticists did not uncover the cause until recently. Dry earwax results from a relatively new mutation to a gene called *ABCC11.* Only 30,000 to 20,000 years old, the mutation also affects the apocrine glands, which produce sweat. If you have stinky armpits and sticky earwax, chances are you have the original version of *ABCC11.* If you have dry earwax and a little less need for deodorant, you probably have the newer mutation.

FINDINGS

The Milk Mutation

Enjoying dairy in adulthood is a privilege that emerged relatively recently in our evolutionary history. We depend on the enzyme lactase to break down lactose, the sugar found in milk, but the human body usually stops producing lactase after adolescence. In fact, most of the world's adults are lactose-intolerant. Within the past 10,000 years, however, different populations of dairy farmers independently evolved genetic mutations that kept lactase active throughout life (lactase persistence). Scientists have identified several such mutations, but there are likely more. Collectively, all these adaptations explain the prevalence of lactose tolerance seen around the world today.


One of the so-called lactase-persistence mutations arose around 7,500 years ago among dairy farmers in a region between Central Europe and the northern Balkans. This is the most common lactase mutation in Europe today.
Data-collection location (*red dots*)
Three different lactase-persistence mutations originated in sub-Saharan Africa, the most common of which spread rapidly through the region in the past 7,000 years.
The world's first dairy farmers lived in the Middle East and North Africa between 10,000 and 8,000 years ago. They primarily raised sheep, goats and cattle, but at least one lactase-persistence mutation likely sprung up among camel herders.
Percent of Adult Population That Is Lactose-Tolerant
10 20 30 40 50 60 70 80 90

THE STORY OF US

A few thousand years before dry earwax first appeared among East Asians, another seemingly simple mutation started saving millions of Africans from a deadly disease. A gene called *DARC* produces a starchy molecule on the surface of red blood cells that mops up excess immune system molecules known as chemokines from the blood. About 45,000 years ago a mutation in *DARC* conferred remarkable resistance to *Plasmodium vivax,* one of the two most prevalent malaria parasites infecting humans today. The vivax parasites enter red blood cells through the DARC molecule encoded by the gene, so hindering the expression of DARC keeps the pathogens at bay. The absence of DARC also increased the amount of inflammation-causing chemokines circulating in the blood, which has in turn been linked to an increase in prostate cancer rates in African-American men. Yet on the whole, the mutation was so successful that 95 percent of people living below the Sahara now have it, whereas only 5 percent of Europeans and Asians do.

THE POWER OF RANDOM

WE ARE ACCUSTOMED TO THINKING about evolution as a process of "good" genes replacing "bad" ones, but the most recent phase of human adaptation is a testament to the power of randomness in evolution. Beneficial mutations do not automatically persist. It all depends on timing and on population size.

I first learned this lesson from anthropologist Frank Livingstone. The beginning of my training coincided with the end of his long career, during which he investigated the genetic basis for malaria resistance. More than 3,000 years ago in Africa and India, a mutation arose in the gene coding the oxygen-transporting blood cell molecule known as hemoglobin. When people inherited two copies of this mutation—dubbed hemoglobin S—they developed sickle cell anemia, a disease in which unusually shaped blood cells clog vessels. Red cells are normally supple and flexible enough to squeeze through tiny capillaries, but the mutant blood cells were rigid and deformed into the characteristic "sickle" shape. As it turns out, changing the shape of red blood cells also thwarted the ability of the malaria parasite to infect those cells.

Another mutation that interested Livingstone was hemoglobin E. Common in Southeast Asia today, hemoglobin E confers substantial malaria resistance without the severe side effects of hemoglobin S. "Hemoglobin E seems like it would be a lot better to have than hemoglobin S," I said in class one day. "Why didn't they get E in Africa?"

"It didn't happen there," Livingstone said.

His reply stunned me. I had supposed natural selection to

SOURCE: GLOBAL LACTASE PERSISTENCE ASSOCIATION DATABASE

Map by XNR Productions

be the most powerful force in evolution's arsenal. Humans had lived with deadly falciparum malaria for thousands of years in Africa. Surely natural selection would have weeded out less helpful mutations and hit on the most successful one.

Livingstone went on to show how the previous existence of hemoglobin S in a population made it harder for hemoglobin E to invade. Malaria rips through a population full of only normal hemoglobin carriers, and a new mutation that provides a slight advantage can quickly become more common. Yet a population already supplied with the protective hemoglobin S mutation will have a lower mortality risk. Sickle cell carriers still face formidable risks, but hemoglobin E is less of a *relative* advantage in a population that already has this imperfect form of malaria resistance. Perversely, what matters is not only the luck of having the mutation but also *when* the mutation happens. A partial adaptation with bad side effects can win, at least over the few thousand years humans have been adapting to malaria.

INSTEAD OF A FEATURELESS MASS OF CAFÉ-AU-LAIT-COLORED CLONES, WE ARE ALREADY STARTING TO SEE A GLORIOUS RIOT OF VARIATIONS—DARK-SKINNED, FRECKLED BLONDES AND STRIKING COMBINATIONS OF GREEN EYES AND OLIVE SKIN.

Ever since humans first began battling malaria, scores of different genetic changes emerged that increased immunity to the disease, different ones in different places. Each started as a serendipitous mutation that managed to persist in a local population despite being very rare at first. Any one of those mutations was, individually, unlikely to last long enough to become established, but the huge and rapidly increasing population size of our ancestors gave them many more rolls of the dice. As human populations have spread into new parts of the world and grown larger, they have rapidly adapted to their new homes precisely because those populations were so big.

OUR EVOLUTIONARY FUTURE

HUMAN POPULATIONS CONTINUE to evolve today. Unlike the distant past, where we must infer the action of selection from its long-term effects on genes, today scientists can watch human evolution in action, often by studying trends in health and reproduction. Even as medical technology, sanitation and vaccines have greatly extended life spans, birth rates in many populations still vacillate.

In sub-Saharan Africa, women who have a certain variant of a gene called *FLT1* and who are pregnant in the malarial season are slightly more likely to bear children than are pregnant women who lack the variant because the possessors have a lower risk that the placenta will be infected by malaria parasites. We do not yet understand how this gene reduces the risk of placental malaria, but the effect is profound and measurable.

Stephen Stearns of Yale University and his colleagues have examined years of records from long-term public health studies to see which traits may correlate with reproduction rates today. During the past 60 years, relatively short and heavy women in the U.S. who have low cholesterol counts had slightly more children on average than women who have the opposite traits. Why these traits have been related to family size is not yet clear.

Public health studies, such as U.K. Biobank, track the genotypes and lifetime health of hundreds of thousands of people. Such studies are being undertaken because the interactions of genes are complicated, and we need to examine thousands of outcomes to understand which genetic changes underlie human health. Tracing the ancestry of human mutations gives us tremendous power to observe evolution over hundreds of generations but can obscure the complex interactions of environment, survival and fertility that unfolded in the past. We see the long-term winners, such as lactase persistence, but may miss the short-term dynamics. Human populations are about to become the most intensively observed long-term experiment in evolutionary biology.

What will the future of human evolution look like? Across the past few thousand years, human evolution has taken a distinctive path in different populations yet has maintained surprising commonality. New adaptive mutations may have elbowed their way into human populations, but they have not muscled out the old versions of genes. Instead the old, "ancestral" versions of genes mostly have remained with us. Meanwhile millions of people are moving between nations every year, leading to an unprecedented rate of genetic exchanges and mixture.

With such a high rate of genetic mixing, it may seem reasonable to expect that additive traits—for example, pigmentation, where many different genes have independent effects on skin color—will become ever more blended in future human populations. Could we be looking at a human future where we are a homogeneous slurry instead of a colorful stew of variability?

The answer is no. Many of the traits that differ between human populations are not additive. Even pigmentation is hardly so simple, as is readily seen in mixed populations in the U.S., Mexico and Brazil. Instead of a featureless mass of café-au-lait-colored clones, we are already starting to see a glorious riot of variations—dark-skinned, freckled blondes and striking combinations of green eyes and olive skin. Each of our descendants will be a living mosaic of human history. SA

John Hawks is an anthropologist and an expert on human evolution at the University of Wisconsin–Madison.

MORE TO EXPLORE

Are Human Beings Still Evolving? It Would Seem That Evolution Is Impossible Now That the Ability to Reproduce Is Essentially Universally Available. Are We Nevertheless Changing as a Species? Meredith F. Small; Ask the Experts, ScientificAmerican.com, October 21, 1999.

African Adaptation to Digesting Milk Is "Strongest Signal of Selection Ever." Nikhil Swaminathan; ScientificAmerican.com, December 11, 2006.

Why We "Got Milk." Andrew Curry; ScientificAmerican.com, July 31, 2013.

scientificamerican.com/magazine/sa

Starship Humanity

How will future generations make the voyage from our earthly home to the planets and beyond—and what will that mean for our species?

By Cameron M. Smith

Illustration by Travis Coburn

WHEN SPACE SHUTTLE *ATLANTIS* ROLLED TO A STOP IN 2011, IT DID not mark, as some worried, the end of human spaceflight. Rather, as the extinction of the dinosaurs allowed early mammals to flourish, retiring the shuttle signaled the opening of far grander opportunities for space exploration. Led by dozens of ambitious private companies, we are entering the early stages of the dispersal of Earth life into the solar system at large. The European Space Agency has revealed plans for a lunar habitat, and a Mars settlement is the stated goal of Elon Musk's SpaceX company. The international research team Icarus Interstellar is taking this century to design propulsion technologies and great starships, ultimately to send an entire culture to a distant exoplanet. The human settlement of space is beginning now.

But technology is not enough. If space settlement is to succeed in the long run, we must consider biology and culture as carefully as engineering. Space settlement cannot be about rockets and robots alone—it will have to embrace bodies, people, families, communities and cultures. We must begin to build an anthropology of space settlement to grapple with the fuzzy, messy, dynamic and often infuriating world of human bioculturral adaptation. And we must plan this new venture while remembering the clearest fact of all regarding living things: they change through time, by evolution.

Three main concepts shape current thought about space settlement. First is the colonization of Mars. Widely publicized by the peppery space engineer and president of the Mars Society, Robert Zubrin, Martian colonies would be self-sufficient, using local resources to generate water and oxygen as well as to make construction materials. Next is the concept of free-floating colonies—enormous habitats built from lunar or asteroid metals. Popularized by physicist Gerard K. O'Neill in the 1970s, these would house thousands of people, could rotate to provide an Earth-like gravity (as beautifully envisioned in the 1968 film *2001: A Space Odyssey*), and could either orbit Earth or hang motionless at so-called Lagrangian points, spots where an object's orbital motion balances the gravitational pull of the sun, moon and Earth. Finally, we might also consider the concept of the Space Ark, a giant craft carrying thousands of space colonists on a one-way, multigenerational voyage far from Earth. I have been working with the nonprofit foundation Icarus Interstellar to design just such a mission.

Each of these approaches has its merits, and I think they are all technologically inevitable. But we must never confuse space colonization with the conquest of space. Successfully settling space beyond Earth will be an enormous challenge. Space is vast and unforgiving. When humanity begins to make its home in space, it is we who will change.

THE PIONEERS

WHO WILL BE THE SPACE COLONISTS? Here we must ditch the old concept of crew selection and the comically diabolical tests of chisel-chinned space heroes depicted in *The Right Stuff*. Space colonists will be ordinary families and communities who will not be on a mission but who are intending to live out their lifetimes. We will need a few Captain Picards, although most early colonists will probably be farmers and construction workers.

Still, early colonists will have to be genetically healthy. In smallish populations, individuals carrying genetic maladies could threaten the future in ways that do not play out in a population of billions. In a Space Ark, the biological fate of the colony is strongly conditioned by the genetic constitution of the founding population—if just a few travelers carry the genes for inherited disease, these genes will spread much more thoroughly.

We now know the details of hundreds of genes that cause disorders, from cancers to deafness. (In 2012 researchers announced that they could screen for more than 3,500 such traits in human fetuses.) A genetic screening program seems clear—if you are carrying certain genes, you remain Earth-bound—but life is not so simple. Many maladies are polygenic—that is, the result of complex interactions among myriad genes. And even though one might carry the gene or genes for a certain disorder, environmental factors encountered during the course of life can

IN BRIEF

A space mission that isolates people away from Earth for extremely long periods—for instance, a Mars colony or a multigenerational voyage to a nearby star—will inevitably lead to the evolution of new cultural and physiological traits.

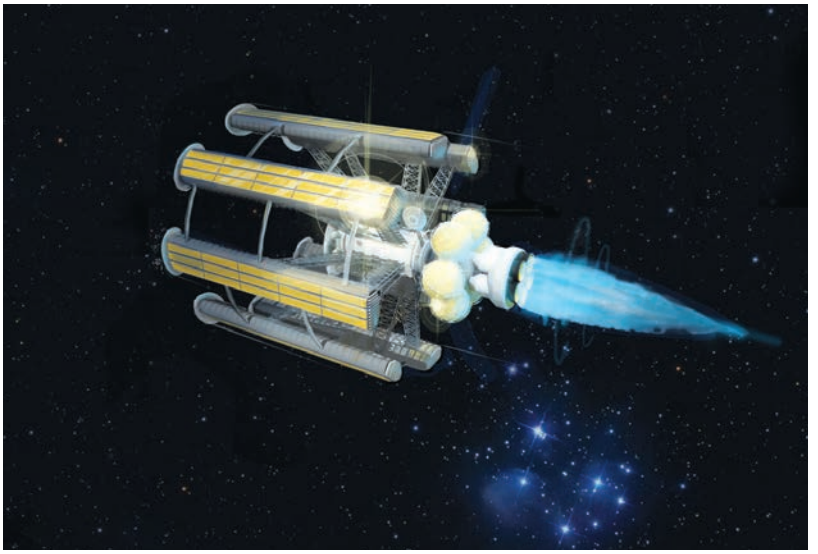
Long-distance spaceships will be home to unique environmental hazards such as increased radiation and lower ambient pressures. These influences will most severely affect the most fragile stages of life—in the womb and just after birth.

Mission planners will have to carefully select the "crew" of space travelers. Their goal: a genetically healthy population but one diverse enough to withstand the occasional pandemic and thrive in profoundly new environments.

determine whether or not those genes are activated in a healthy or unhealthy way.

For example, the human *ATRX* gene helps to regulate processes related to oxygen transportation. But *ATRX* activity can be altered by environmental influences as diverse as nutrient intake or a person's state of mind. When *ATRX* function is significantly modified, oxygen transport is impeded, resulting in seizures, mental disabilities and stunted growth. Thus, one cannot simply screen out people carrying *ATRX:* everyone has it. In some people, though, based on poorly understood environmental factors, *ATRX* will go haywire. Can we deselect someone for space colonization for something that *might* happen?

Complicating matters, we must also ensure broad genetic diversity of the gene pool. If all members of a population are genetically identical, a single sweep of disease could wipe everyone out. (This consideration demolishes the concept of a genetically engineered superrace of space travelers, as depicted in the 1997 film *Gattaca*.)



SHIP SHAPE: Interstellar spacecraft will have to carry thousands of people, plus the plants and animals needed to support them.

Once screened, what should be the population of space colonies? In a Mars colony, populations can grow and expand into new territory. But in a Space Ark, the population will be relatively low, and inbreeding becomes a concern. For example, in a study of Amish, Indian, Swedish and Utah populations, infant mortality was roughly double when matings occurred between first cousins than when they occurred between unrelated people.

To avoid these issues, we will have to consider the minimum population needed to maintain a healthy gene pool. Our minimum viable population has been much debated, but several anthropologists have suggested a figure of about 500. Because small populations are always at greater risk of collapse, I would suggest beginning with a population at least four times that at minimum—2,000, or about the population of an English country village—in a spacecraft that gives this population ample room to grow. For humans away from Earth, safety will indeed be found in numbers. (Even interstellar voyages will focus on reaching another solar system and inhabiting its planets, where populations can grow again.)

We will also have to carefully consider the colonists' demographic structure—the age and sex of colonial populations. Simulations by my colleague William Gardner-O'Kearney show that over a few centuries, populations that begin with certain ratios of young to old and males to females persist better than others.

Early colonial populations, then, should be individually healthy and collectively diverse to give future populations the best chance of having genes on hand that might be adaptive in new environments. But we cannot control everything. At some point we will have to roll the genetic dice—which we already do every time we choose to have children on Earth—and set out from our cradle planet.

SPACE-BASED SELECTION

NO MATTER HOW CAREFULLY we prepare our colonial populations, life off planet Earth, at least at first, will be more dangerous and perhaps shorter than life here. Away from Earth, people will be exposed to forces of natural selection that we have technically all but removed from modern life. Little of this selection will play out in the dramatic ways we might expect from science-fiction movies, which tend to focus on the lives of adults. Instead it will occur during critical periods of tissue development in embryos and infants, when life is most delicate.

How could such selection play out? As one example, consider that the human body has evolved close to sea level under an atmospheric pressure of roughly 15 pounds per square inch (psi) for the past several million years, breathing a mix of roughly 80 percent nitrogen and 20 percent oxygen. Yet space travel requires pressurized habitats that grow more expensive and laborious to build the more pressure they need to hold. To ease the engineering requirements, atmospheric pressure in any off-Earth structure will be lower than on Earth.

Fair enough—*Apollo* astronauts survived just fine at 5 psi—but if you lower atmospheric pressure, you must increase oxygen as a percentage of what you are breathing. (Those same astronauts breathed 100 percent oxygen on their lunar voyages.)

Unfortunately, lower atmospheric pressure and elevated oxygen levels both interfere in vertebrate embryo development. Miscarriages and infant mortality will rise—at least for a time. Inevitably, selection will preserve the genes suitable for extraterrestrial conditions and remove those that are less suitable.

Infectious disease—to which small, dense populations such as space colonies are particularly vulnerable—will return as a significant concern, imposing new selection pressures as well. However careful we are with immunization and quarantine, plagues will eventually sweep through colonies, resulting in selection for people more capable of surviving the disease and selection against those less capable.

Finally, we must remember that we bring with us thousands of domesticates—plants and animals for food and materials—and that selective pressures will act on them as well. Ditto the millions of microbial species that ride on and in human bodies—

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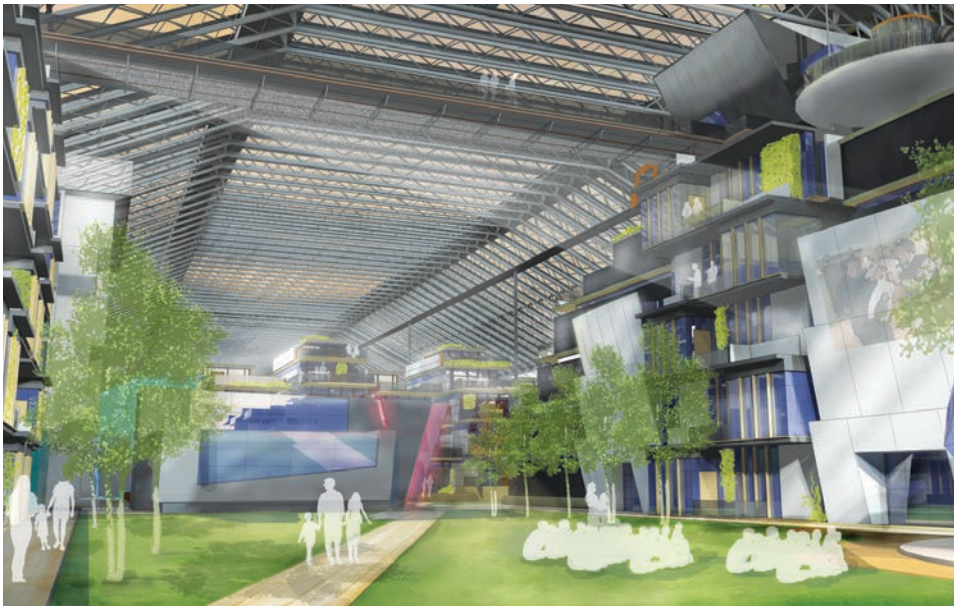
invisible genetic hitchhikers that are critical to our health.

Based on a few calculations, I think it is reasonable that within five 30-year generations—about 150 years—such changes will be apparent in the extraterrestrial human body.

Exactly what biological adaptations evolve will depend heavily on the atmospheric and chemical environments of the habitats we build. We can control these to a large extent. Yet we cannot easily control two other important factors that will shape humanity in space: gravity and radiation.

Mars colonists will feel just a third of Earth's gravity. Over generations, without Earth's gravity, a heavier build will probably be replaced with a lighter, lither Martian stature. In Space Ark and other free-floating scenarios, gravitation might remain about Earth normal, so Earth-normal statures might persist.



SPACE LIFE: We cannot predict how the culture of a space outpost will change over hundreds of years—only that it will.

Radiation causes mutations, and any space colony will be unlikely to provide the protection from radiation that Earth's atmosphere and magnetic field provide. Will increased mutations create physical errors—repeated parts like an extra finger or malformed parts like a cleft palate? Certainly, but we cannot know what kind. The only thing we can predict with confidence is selection for increased resistance to radiation damage. Some people have better and more active DNA-repair mechanisms than others, and they will be more likely to pass their genes on.

Could more efficient DNA-repair mechanisms have any visible correlate—such as, say, a particular hair color? Again, we do not know. But it is also possible for beneficial genetics to spread when they have no such visible correlates. Among Hutterites of South Dakota, who interbreed among a relatively small number of small communities, anthropologists have found that people appear to be strongly influenced in their mate choice by body aroma—and the better the person's immune system, fascinatingly, the better the aroma.

On a moderate, five-generation timescale, then, human bodies will be subtly reshaped by their environment. We will see the origins of adaptations on the order of those of the natives of the high Andes and Tibet, where a more efficient oxygen-transport physiology has evolved, resulting in broader and deeper chests. Each alteration is a compromise, however, and these high-altitude populations also sustain higher infant mortality when giving birth at altitude. One cultural adaptation to this biological change has been for mothers to descend to oxygen-richer altitudes to deliver children. We can expect similar biocultural shifts off of Earth, and we should plan for the most likely of them. For example, on Mars, birthing mothers might shuttle to an orbiting station where delivery could happen in a rotating, 1-g facility with a more Earth-normal atmosphere, but I bet that eventually they would not bother and that distinctive Martian human characteristics would evolve.

A SPACE-BASED CULTURE

CULTURAL CHANGE will be more apparent than biological change on a 150-year time span. Studies of human migrations have taught us that while migrating peoples tend to carry on some traditions to maintain identity, they also devise novel traditions and customs as needed in new environments. For example, the Scandinavians who first colonized Iceland after A.D. 800 continued to worship Norse gods and speak the Viking language but quickly developed a distinctive cuisine—heavy on meat (whereas rye and oats were grown in Scandinavia) and on preserved foods to survive the harsh winters—as they explored the resources of an unknown land.

On Mars, this acculturation will play out in innumerable ways. There, in low-pressure, oxygen-rich atmospheres contained in unique architectural materials and arrangements, sound might propagate differently—even if subtly—perhaps affecting pronunciation and even the pacing of speech, resulting in novel accents and dialects. The lighter gravity could influence body language, an important element of human communication, and would influence performance arts of all kinds. Cultural divergence occurs as just such small, innumerable differences accumulate.

More profound cultural change could occur in Space Ark scenarios, where life would have less to do with Earth at each moment that the starship speeds away. Here basic concepts of space and time could well be transformed rather quickly. For example, how long would Space Ark cultures use Earth timekeeping? Without Earth's days and nights and years, civilizations might invent a base-10 timekeeping scale. Or they might decide to count time down until a distant solar system is reached rather than up from some event in the past (such as the departure from an Earth to which they will never return).

LONG-TERM GENETIC CHANGE

SIGNIFICANT GENETIC CHANGE occurs when new genes become widespread in a population. An example from prehistory is the

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spread of genes that resulted in lactose tolerance in adults, which appeared independently in both Africa and Europe not long after the domestication of cattle. This genetic equipment allowed more energy to be derived from cattle, and in these populations, it quickly became nearly universal, or "fixed."

Although we cannot predict which mutations will arise, population genetics enables us to estimate how long it would take mutations to become fixed in the genome of space-based explorers. My calculations—based on model Mars populations of 2,000 people of certain age and sex structures—indicate that it could occur in just a few generations and certainly within 300 years; we can expect subtle original off-Earth physical characteristics in human populations on this timescale. These changes will be on the order of the broad geographical variation we see in humans today—variation in statures, skin colors, hair textures and other features.

On Mars, there might be further, internal divergence as some populations elect to live most of their lives sheltered in underground habitats, while others prefer to take the increased radiation risks to live in surface habitats offering greater mobility. In the limited-population, closed-system Space Ark scenario, gene fixation could happen much more rapidly, perhaps driving a greater uniformity than on Mars.

Whereas there will be some biological change, long-term cultural change will be more profound. Consider that in the three centuries from the early 1600s to the early 1900s, the English language changed so much that comprehending 17th-century English texts today requires special training. Three centuries hence, the language spoken on a Space Ark might be profoundly different.

Larger-scale cultural change is also quite likely. Exactly what divides one culture from another is a topic of tremendous debate in anthropology, but I believe that anthropologist Roy Rappaport made the distinction clear. Different cultures have different "ultimate sacred postulates"—core concepts, usually unquestionable and unquestioned, ingrained by tradition and ritual, that shape a population's essential philosophical and moral codes. For Christianity, for example, one such postulate is that "In the beginning, God created the heaven and the Earth." How long it will take for such foundation beliefs to change off of Earth—and in what direction—is impossible to say, but several centuries is certainly enough time to allow new cultures to arise.

THE EVOLUTION OF *HOMO EXTRATERRESTRIALIS*

WHEN WILL WE SEE even more fundamental biological change—that is, speciation? Small populations can change quickly, as evidenced by the unusually large mice that roam the Faroe Islands 1,200 years after Viking ships dropped off ordinary house mice. But anatomically modern humans have gone more than 100,000 years—migrating from Africa into a wide variety of environments, from desert to open ocean—apparently without biological speciation. (Our nearest hominin relatives, such as the cold-adapted Neandertals and the apparently miniaturized "hobbit" humans of the island of Flores in the western Pacific, split from our common ancestor substantially earlier.) This is largely because we use culture and technology to adapt more than biology alone. It would take, then, significant natural and cultural selection to reshape extraterrestrial humans to such a degree that they could no longer productively mate with earthlings.

Unless, of course, humans devise their own speciation. It seems inevitable that off-Earthers will eventually harness the staggering power of DNA to tailor their own bodies for many conditions. Our distant descendants on Mars might biologically engineer gill-like structures to split the oxygen from atmospheric carbon dioxide—a process NASA is currently investigating—and skin tissues that could endure low surface pressure. They might tailor themselves into a new species, *Homo extraterrestrialis,* by conscious choice.

WHERE TO BEGIN?

HUMAN SPACE COLONIZATION will require plenty of engineering and technical advances. We must also improve our understanding of how human biology and culture adapt to new conditions and use that knowledge to help space colonization succeed. I suggest beginning immediately with three courses of action.

First, we must abandon the technocrat's essential revulsion of humanity and begin procreating off of Earth, giving birth there and raising children there, to understand critical issues of human reproduction, development, and growth in new radiation, pressure, atmospheric and gravity environments. Bureaucrats will recoil at the risks involved—children exposed to risk beyond that of a bicycle-helmeted, First World suburbanite!—but concerns will diminish as space access is privatized. Still, at times the adaptation to space will be painful—but so is birth.

Second, we must experiment with growing and maintaining the health of domesticated species off of Earth. We are going nowhere without our microbes, plants and other animals.

And to promote these first two goals, an X-Prize should be awarded for the first functional, livable human habitat off of Earth: not a sterile orbiting laboratory (as important as those are) but a home where people can grow plants, raise animals and even have children. Many would shudder at the prospect of staying in such a place, but at the same time, there will be no shortage of volunteers.

Finally, we must reengage the proactive approach that has made human survival possible up to the present and use that capacity to shape our own evolution beyond our home planet. We must be immensely bolder than our bureaucracies. Failing that, in time we will become extinct, like everything else on Earth. As H. G. Wells wrote about the human future in 1936, it is "all the universe or nothing." SA

Cameron M. Smith teaches human evolution at Portland State University. He has written about evolution in *Scientific American Mind* and in his books *The Fact of Evolution* (Prometheus Books, 2011) and *Emigrating Beyond Earth* (Springer Praxis Books, 2012).

MORE TO EXPLORE

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END NOTE

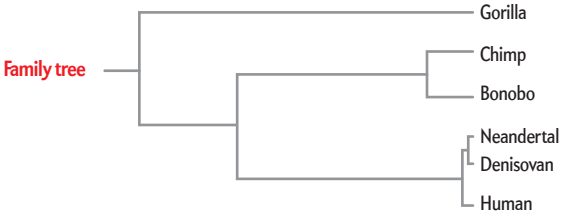
The 1 Percent Difference

Genome comparisons reveal the DNA that distinguishes *Homo sapiens* from its kin

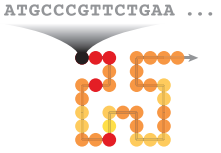
In 1871 Charles Darwin surmised that humans were evolutionarily closer to the African apes than to any other species alive. The recent sequencing of the gorilla, chimpanzee and bonobo genomes confirms that supposition and provides a clearer view of how we are connected: chimps and bonobos in particular take pride of place as our nearest living relatives, sharing approximately 99 percent of our DNA, with gorillas trailing at 98 percent.

Yet that tiny portion of unshared DNA makes a world of difference: it gives us, for instance, our bipedal stance and the ability to plan missions to Mars. Scientists do not yet know how most of the DNA that is uniquely ours affects gene function. But they can conduct whole-genome analyses—with intriguing results. For example, comparing the 33 percent of our genome that codes for proteins with our relatives' genomes reveals that although the sum total of our genetic differences is small, the individual differences pervade the genome, affecting each of our chromosomes in numerous ways.

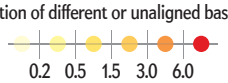
—Kate Wong

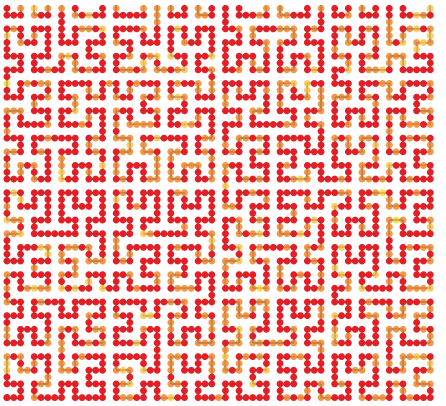


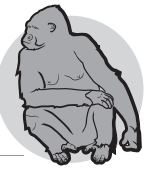
Each dot represents a sequence of about 500,000 pairs of chemical bases—the A, T, C and G of our genetic code—in the protein-coding portion of the human genome in the order that they appear on our chromosomes.



The color of the dot indicates how well the human sequence matches up with the corresponding sequence in the comparison species, with red signifying a greater difference between the two.

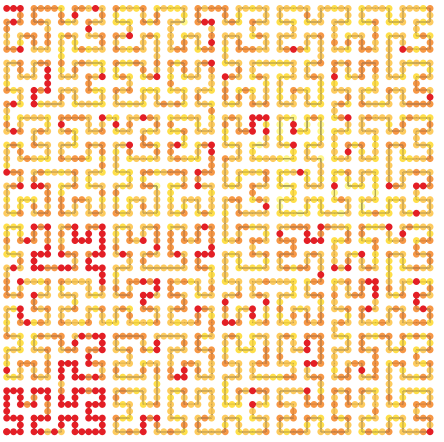






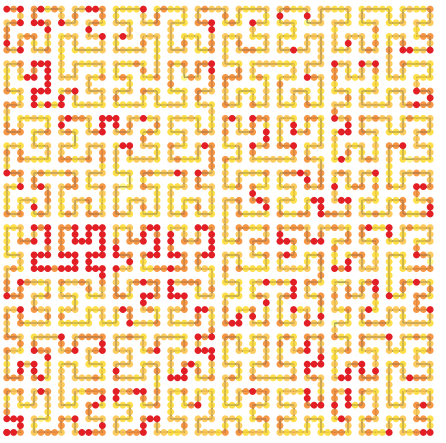
Gorilla

On the whole, our coding genome differs more from the gorilla's than from the chimp's or the bonobo's, reflecting the fact that we have been evolving along separate trajectories for a longer period. But about 15 percent of the human genome looks more like the gorilla's than the chimp's or the bonobo's.



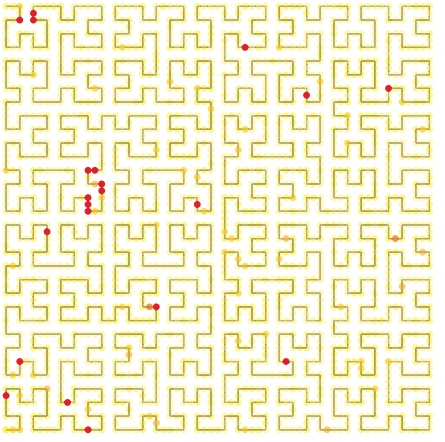
Chimp

Researchers have traditionally considered the chimpanzee, which lives in patriarchal societies, to be our closest living relative and thus the best model for reconstructing the lives of ancient human ancestors. The recent genome-sequencing work calls that view into question, however.



Bonobo

The genome of the bonobo—which has a social structure centered on females—shows it to be just as closely related to us as chimps are, although we differ from the two species in distinctive ways. These findings may force scientists to reconsider how our long-ago forerunners lived.



Denisovan

The Denisovans—a group of archaic humans closely related to the Neandertals—show far fewer sequence differences from us than any of the African apes do, having shared a common ancestor with *H. sapiens* in the much more recent past, around 400,000 years ago.

SOURCES: UNIVERSITY OF CALIFORNIA, SANTA CRUZ, GENOME BROWSER (*chimp, gorilla and bonobo data*); MAX PLANCK SOCIETY (*Denisovan data*); "INITIAL SEQUENCE OF THE CHIMPANZEE GENOME AND COMPARISON WITH THE HUMAN GENOME," BY CHIMPANZEE SEQUENCING AND ANALYSIS CONSORTIUM, IN *NATURE*, VOL. 437; SEPTEMBER 1, 2005; "INSIGHTS INTO HOMINID EVOLUTION FROM THE GORILLA GENOME SEQUENCE," BY AYLWYN SCALLY ET AL., IN *NATURE*, VOL. 483; MARCH 8, 2012; "THE BONOBO GENOME COMPARED WITH THE CHIMPANZEE AND HUMAN GENOMES," BY KAY PRÜFER ET AL., IN *NATURE*, VOL. 486; JUNE 28, 2012; "A HIGH-COVERAGE GENOME SEQUENCE FROM AN ARCHAIC DENISOVAN INDIVIDUAL," BY MATTHIAS MEYER ET AL., IN *SCIENCE*, VOL. 338; OCTOBER 12, 2012

Graphic by Martin Krzywinski, Illustrations by Portia Sloan Rollings